ACTA PHYTOGEOGRAPHICA SUECICA 64
EDIDIT
SVENSKA VÄXTGEOGRAFISKA SÄLLSKAPET

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Vegetation and local environment on shore ridges at Vickleby, Öland, Sweden. An analysis

UPPSALA 1978

Suggested citation: Ammar, M.Y., 1978, Vegetation and local environment on shore ridges at Vickleby, Öland, Sweden. An analysis. Acta Phytogeogr. Suec. 64. Uppsala.

Doctoral dissertation at Uppsala University, Sweden 1978.

ISBN 91–7210–064–8 (paperback)
ISBN 91–7210–464–3 (cloth)

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Svenska Växtgeografiska Sällskapet
Box 559, S–751 22 Uppsala

Editor: Erik Sjögren
Technical editor: Gunnel Sjörs

Phototypesetting by
TEXTgruppen i Uppsala AB

Printed in Sweden 1978 by
Borgströms Tryckeri AB, Motala

Acta Phytogeogr. Suec. 64

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Vivi Laurent Täckholm

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Preface

The present work has been carried out at the Institute of Ecological Botany, University of Uppsala, under the supervision of Erik Sjögren and Hugo Sjörs. I wish to express my sincere gratitude both to the head of the Institute Hugo Sjörs and to Erik Sjögren for their guidance, encouragement, advice, and critical scrutiny, and also for examining the entire MS.

The object for this investigation was suggested by Erik Sjögren. He kindly examined all stands and permanent sample plots. Furthermore, he helped with identification of all bottom layer species and provided valuable general information about the study area. I appreciate very much his suggestions and discussions throughout this study.

All field work was based at the Ecological Station of the University of Uppsala, on Öland. I am most grateful to its director, Bertil Kullenberg, for his great hospitality and encouragement. My thanks are also extended to all members at the Station who kindly helped in different ways.

I owe very much to Eddy van der Maarel and Jo M. Louppen (Dept. of Geobotany, University of Nijmegen) for their hospitality and help with computerization of my data. The computerization costs were generously payed for by the University of Nijmegen. Eddy van der Maarel once visited my study area. His stimulating interest and our fruitful discussions became important for the preparation of the MS.

Björn Widén (Dept. of Systematic Botany, University of Lund) helped with identification of some plants, and Ruth Oswald at SLL (Agricultural University, Uppsala) took care of some soil analysis.

Lars-König Königsson (head of the Dept. of Quaternary Geology, University of Uppsala) made corrections in the section on "Geology and soils".

I had many valuable discussions of my study with Ejvind Rosén (Inst. of Ecological Botany, University of Uppsala). He became my first friend in Sweden and helped me and my family in various ways.

At the same Institute Sven Bråkenhielm, Hans Persson, Willy Jungskär and Tord Ingmar, among others, offered valuable discussions and good pieces of advice. Märta Ekdahl patiently and efficiently typed the entire MS including all the tables. Folke Hellström kindly assisted with photography work and Agneta Nordgren with drawing of diagrams. Åke Sjödin and Salme Sedman generously helped with references.

My wife Samia Ammar kindly helped with sorting of plant material for the determinations on productivity. Her patience and support with my work, as well as in other ways, are sincerely appreciated.

Margaret Jarvis (University of Edinburgh) read the MS critically and made valuable suggestions from a linguistic point of view.

Gunnel Sjörs and Erik Sjögren made the editorial work.

My sincere thanks go to all persons mentioned above and many other friends at the Inst. of Ecological Botany and elsewhere who in some way or other participated in my studies.

This study was made possible by a scholarship award from the government of the Arab Republic of Egypt. The co-operation and supervision of our Egyptian education and mission Bureau at Bonn should also be mentioned. The financial assistance from the University of Uppsala covering costs for field work is also highly acknowledged.

Uppsala April 1978

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Ammar, M.Y., 1978, Vegetation and local environment on shore ridges at Vickleby, Öland, Sweden. An analysis. Acta Phytogeogr. Suec. 64. Uppsala. 96 pp.

The vegetation and environment on three former shore ridges, the Ancylus, the Litorina and the "Recent" ridge, at Vickleby on the limestone island of Öland (Sweden) were investigated quantitatively. 73 stands were objectively selected, within 2 km, in order to include as much variation as possible in species composition, light, moisture, canopy cover, elevation, and grazing influence. The vegetation was found to be unstable and heterogeneous.

Multivariate analyses (principal components analysis, PCA, and agglomerative classification) were complementary and provided insight into factors controlling the vegetation as well as phytosociological groups. These groups were interrelated but distributed along a successional gradient with stages of increasing stability.

The vegetation structure of the ridges as a whole, as well as on each individual ridge, was considered as a continuum. Canopy cover, light and moisture appeared to be of overriding importance, being generally related to the successional sequence.

Disturbance by man and animals has influenced the vegetation for centuries, and tourist trampling and short periods of grazing occur today, obscuring edaphic relationships. Edaphic characters varied significantly in horizontal and vertical directions between the stands with regard to soil depth and drainage.

The annual above-ground production was estimated over the years 1975—77 as 336.5, 339.2 and 445.9 g/m^2 for three open dry meadow plots on the Ancylus, Recent, and Litorina ridges, respectively, and as 185.1 g/m^2 for the field layer of a low-cover forest plot on the Litorina ridge. The values for each year suggest strong correlation with rainfall. The cessation of grazing was found to lead to successional changes. Grazing management for conservation is discussed.

Local climate varied between vegetational types and between the ridges. Changes of vegetation were followed over the years 1975—1977 in open meadows and forest plantations, being affected by climatic fluctuations. A main trend of succession is outlined.

Abbreviations

PCA	Principal components analysis
A	Ancylus ridge
L	Litorina ridge
R	Recent ridge
ALR	All ridges together
H.M.	Hygroscopic moisture
W.H.C.	Water holding capacity
O.M.	Organic matter
N_{tot}	Total nitrogen
Cond.	Conductivity
C.E.C.	Cation exchange capacity
T.E.B.	Total exchangeable bases
T.A.	Titratable acidity
H_0	The surface (upper) soil horizon
H_1	The lower soil horizon
SD	Standard deviation
RH	Relative humidity (%)
T	Temperature (°C)

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Introduction

Studies concerned with vegetation-environment relationships have been carried out on the shore ridges in Vickleby (Sjögren 1954a, 1961 and 1964; Ekstam & Sjögren 1973). However, these studies were restricted to a few small areas and dealt mainly with the bryophyte vegetation in deciduous woods.

Little information was available about micro-environmental variation and micro-structure of the vegetation on these shore ridges. More detailed studies of this vegetation were needed to elucidate its structure and explore the principal controlling environmental factors, since there were no quantitative data on environmental gradients. The present work attempts to quantify as many environmental parameters as possible in order to determine some of the more subtle vegetation-environment relationships. Furthermore, it includes an attempt to classify and ordinate the vegetation.

The work presented here was carried out in 1975–77 and was designed to provide a quantitative analysis of the vegetation and environmental micro-variations on the shore ridges.

The aims of the study were as follows:

(1) To determine the phytosociological structure of the vegetation on each individual ridge and of the vegetation of the three ridges as a whole.
(2) To provide a quantitative assessment of the main environmental factors.
(3) To identify the major factors or interrelated groups of factors controlling the differentiation of vegetation in the study area.
(4) To evaluate the relationships between vegetation and environmental factors.
(5) To indicate whether the vegetation is divisible into phytosociological groups and then to characterize these groups.
(6) To follow the changes of vegetation in some permanent sample plots.
(7) To estimate the productivity in order to suggest a grazing management plan.

Microclimatic conditions are affected by aspect, slope and the canopy and lower vegetation cover at a site. They include local variations in irradiation, temperature, moisture, etc. For convenience, the term "microclimatic factors" in the following describes the assemblage of canopy cover, light, and moisture factors.

Study area

Geology and soils

The island of Öland is situated in the Baltic sea (Fig. 1) close to the SE coast of the mainland of Sweden. It is about 130 km long and at most 16 km wide. There are two main ridge systems (Fig. 2) apparent in the landscape of the western side of the island; they can also be detected along the eastern side. These ridges run roughly parallel to each other and to the present shore line, in a N-S direction.

Öland first appeared in the Late Pleistocene and was repeatedly partly flooded and exposed during the various stages of the Baltic. This resulted in littoral deposits and shore ridge systems; the two main shore ridge systems, Ancylus and Litorina, are derived from the Ancylus Lake and the Litorina Sea, respectively. In the area between the Litorina ridge and the present shore line additional ridges are clearly detectable in some places (cf. Königsson 1967, 1968a, b), but in the study area only one ridge formation, here termed the Recent ridge, can be distinguished.

The bedrock of most of Öland is Ordovician limestone but in the western parts of the island sand- and siltstones of Cambrian age appear. The structure of the limestone bedrock controls the main features of the generally extremely flat topography of central Öland. When the land ice disappeared from what is now Öland, tills and glaciofluvial deposits remained on the bedrock. These Quaternary deposits are mostly very thin and the water economy of the soil is often critical. The ridges dealt with are situated beneath the western escarpment of the central plateau.

Königsson (1968b) made a preliminary contribution to evaluating the ages of the ridge systems, especially on the eastern side of the island. His investigation is still going on, using ^{14}C-isotope and pollen analysis. He made a rough estimate of the age of the Ancylus ridge as 8–9 thousand years, and that of the Litorina ridge as 6.5–6 thousand years, from his ^{14}C-studies of material collected from the ridge systems on eastern Öland. Similar results have recently been published from Estonia (Kessel 1977). Little or nothing is yet known of when the additional ridges found close to the shore line were formed. However, investigations of the younger ridge systems are in progress (L.-K. Königsson, pers. comm.). It can be concluded that the ridge systems were formed at well-separated geological times. The name "Recent ridge" has been used to distinguish the young ridge, or rather ridge system, near the coast from the two older ridges (Ancylus and Litorina).

The study area (Figs. 1 and 2) is situated in the SW part of the island, in the parish of Vickleby. The shore ridges there are quite well separated and do not overlap, as they do in several places on the island. The topography of each ridge is fairly homogeneous within the parish. The highest parts are almost uniformly flat.

The stands selected for study are distributed along the three ridges in a N to S direction and are a maximum of 2 km apart. The height of the ridges varies from 2 to 15 m above sea level. The uppermost parts of the deposits are mainly sandy (> 90 % in the

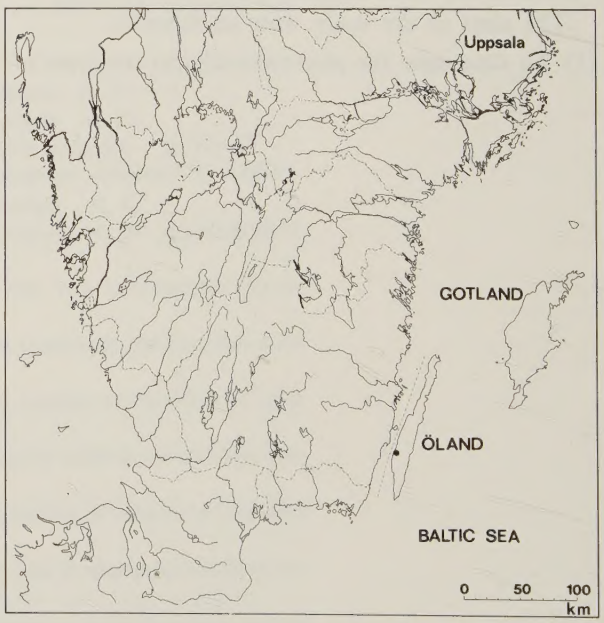


Fig. 1. The position of the study area on the island of Öland in the Baltic.

three sand fractions of the sieved material $\leqslant 2$ mm; see soil sampling and analysis). Stones and boulders are abundant especially on the Recent ridge. The materials are free or almost free of $CaCO_3$, at least down to 40 cm, and are slightly acid. The uppermost layer is fairly deep on the Ancylus ridge but shallower on the Litorina and Recent ridges.

Climate

Unfortunately, there is no special study available of weather conditions or classification of the climate of Öland. Sjögren (1961) and Königsson (1968a) summarized some information about the climate of Öland. The climatic data used in determining the type of climate in the study area were recorded at the Mörbylånga Sugar Company Meteorological Station. This is the nearest official station, south of the study area and at almost the same altitude.

The mean annual precipitation was calculated for the period between 1958 and 1977 as 473.9 $\pm$ SD (99.5) mm. Sjögren (1961) gave the figure 461 mm for the average annual rainfall for the period 1945–1956 and Bergsten (1955) gave 441 mm for 1901–1930 at the same station. These figures are typical of the east coast of Sweden but lower than in most of the rest of the country (Ångström 1974). According to Sjögren (1961), the average precipitation for the period April to September is 235 mm, which is a critical limit for cultivation without irrigation on Öland. The number of days with snow cover was estimated as less than 40 in the southern parts of the island which has very little snow (Ångström 1974).

Öland has been regarded as semi-arid, because of its situation in the rain-shadow of the nearby mainland, but in an international context this is an exaggeration.

The average temperature for the period 1935–1947 was calculated by Sjögren (1961) to be 7.4°C and by Bergsten (1955) to be 6.6°C for 1901–1930 at the same station. February is the coldest month with an average temperature between −2 and −1°C while July is the warmest month with an average temperature between +16 and +17°C (Ångström 1953). The mean number of sunshine hours per year is 2000, which is a high figure in comparison to the 1600 hours recorded in parts of SW Sweden (Königsson 1968a). Temperature climatic conditions are more maritime than on the Swedish mainland nearby.

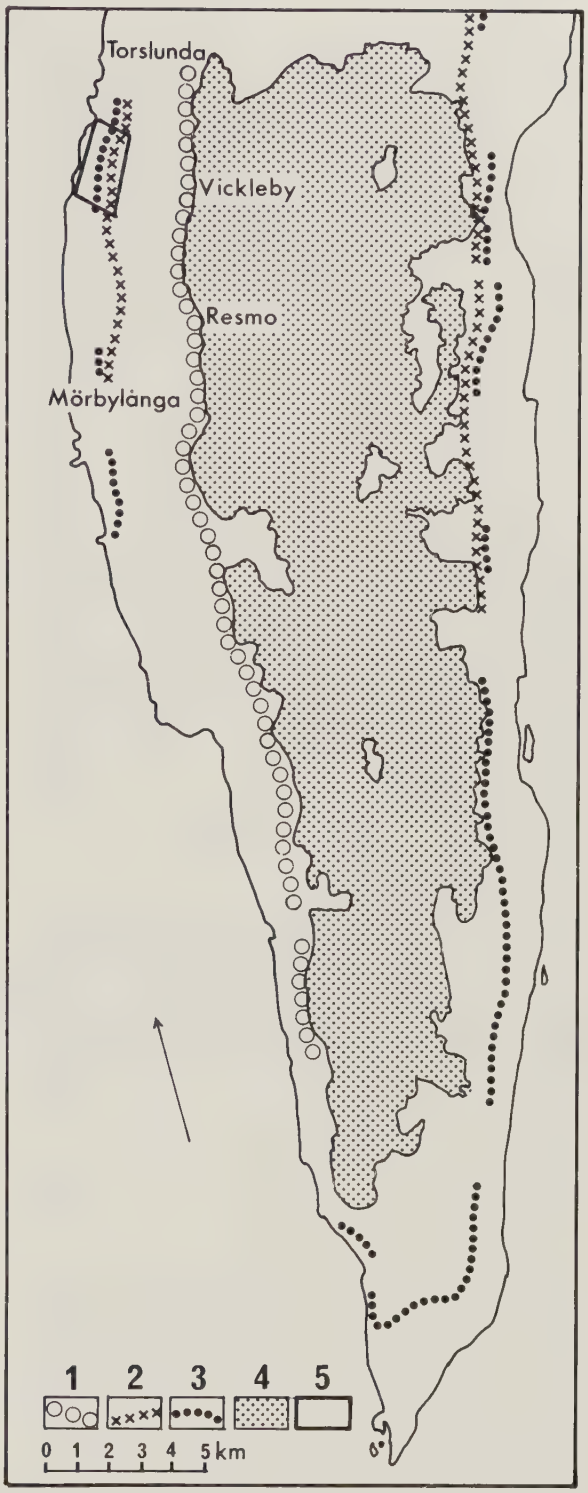


Fig. 2. Southern Öland with the diagramatic position of the study area and the shore ridges. Symbols: 1. Ridge on top of the escarpment (Klint); 2. Ancylus ridge; 3. Litorina ridge; 4. The Great Alvar with limestone heath vegetation; 5. Study area. (Redrawn from Königsson 1968a, p. 49.)

The prevailing wet summer winds are mainly SW to WNW (Östman 1926).

The investigated period was climatically abnormal in several respects. Comparison with annual long-term averages (at least for 20 years) shows that in 1975 the rainfall was exceptionally low and the mean temperature very high (Table 1). It is apparent from the table that weather conditions varied considerably during the years of the study. For example, May 1975 was very wet (60.4 mm precipitation), while December 1975 was the driest month of that year (4.2 mm). However, in 1976 December was the wettest month. On the other hand, May was the second driest month in 1977 (precipitation 23.7 mm) while July was the wettest (79.7 mm). The recorded temperatures also varied considerably from year to year for the same months during the study period. Furthermore, the number of days with snow-fall was different in 1975–1977 (20 days in 1975 but 52 in 1976). Fluctuations in the Öland climate were thus considerable not only from year to year but also within much shorter periods of time (see also Table 7).

Vegetation

The parish of Vickleby can be divided into two parts, separated by an escarpment, the "Klint", running parallel to and well above the shore ridge systems (Fig. 2). The eastern part is dominated by the flat limestone heath vegetation of the so-called "Alvar". The western part extends to the present shore line. It includes shore ridge vegetation, arable fields and areas between the ridges, mainly with remains of wooded meadows, unmanaged wet deciduous forest and a few small forest plantations.

The present-day shore ridge vegetation is richly varied, comprising managed and unmanaged open meadows, wooded meadows, unmanaged deciduous forest, *Betula verrucosa* and *Pinus sylvestris* plantations and mixed forests. The shore ridge vegetation reflects stages in a long and complicated development. These stages have been outlined by Ekstam & Sjögren (1973) in a paper on the deciduous forest of the last four centuries in Vickleby parish; see also the discussion by Göransson (1969) on arable fields, meadows and range areas on the island of Öland.

Ekstam & Sjögren have shown four stages of distribution of vegetation in the western part of Vickleby parish, using information on old geometric maps of the parish (op. cit., Fig. 1 a–d).

(1) 17th century: The description of vegetation which accompanied the map of 1682 stated that "The meadow is large and reaches the coastlines. Parts are, however, covered by dense forest and are impossible to harvest". The managed wooded meadows were of great importance in providing harvested fodder for the cattle. The total area of arable fields in the parish was 105 hectares, only about 14 % of the present area.

(2) 18th century: In documents accompanying the map of 1738, areas east of the Ancylus ridge were described as: "Meadow in part densely covered by hazel, hawthorn, lime and oak; only half the area can be used for the hay harvest." Also it is stated that: "Almost the whole area is covered by oak, hazel, lime and hawthorn." Not more than 1/3–1/4 *palm* of hay could be obtained from one hectare. Documents attached to 18th century maps classified the meadows of the parish as dry meadows (66 % of the total) and moist meadows (12 %).

The floristic research began with Linnaeus and his famous journey to the island in 1741. In his description from the parish of Vickleby (4th June), he writes: "The route ran through the most beautiful groves we ever saw which in loveliness by far surpassed all places in Sweden and rivalled all in Europe; they were composed of lime, hazel and oak with an even and green sward without stones or mosses; here and there we saw the finest meadows and fields." Species mentioned by Linnaeus were: *Milium effusum, Dentaria bulbifera, Mercurialis perennis, Alliaria petiolata* and *Primula farinosa*. The latter two species were not recorded in the present ridge vegetation.

(3) 19th century: The local law against tree felling from 1569 was repealed. Grazing and hay production were intensified to meet the rapid increase in number of inhabitants in the parish and it became necessary to clear the dense forest. Meadows to the west of the Ancylus ridge were probably commonly managed by the farmers between 1866 and 1890.

(4) 20th century: The cultivation of fodder crops on arable fields (leys) began and became essential to meet the rising demand for cattle fodder; grazing was maintained only for short periods of the year in the forest. In 1937 grazing decreased by 70 % and large areas in the western part of the parish were purchased by the Swedish Sugar Company Ltd. After that, cattle grazed almost only on cultivated pastures and

recolonization by trees and shrubs began. Cultivation of conifers began at the beginning of the century and has locally changed the appearance of the parish.

According to the classification by Sjögren (1961, 1964) and Ekstam & Sjögren (1973), the vegetation on the slopes of the shore ridges may be differentiated in the following way. In the *Quercus robur-Betula verrucosa* woods with *Corylus avellana* there is a predominant *Poa nemoralis* - alliance in the field layer. *Poa nemoralis, Maianthemum bifolium, Stellaria holostea, Luzula pilosa, Melampyrum pratense, Oxalis acetosella, Melica nutans,* and *Veronica chamaedrys* are differential species. In the *Quercus robur-Betula verrucosa* woods with *Juniperus communis* the field layer consists mainly of a *Deschampsia flexuosa-Hypericum perforatum-Veronica officinalis* - alliance. *Deschampsia flexuosa, Hypericum perforatum, Veronica officinalis, Antennaria dioeca, Jasione montana, Hieracium pilosella, Viscaria vulgaris, Luzula campestris,* and *Calluna vulgaris* are differential species. These low dry oak-woods occur mainly on sandy soils on and near the Ancylus and Litorina ridges. In the *Fraxinus excelsior-Ulmus glabra* woods the *Mercurialis perennis* alliance is predominant. The differential species include *Mercurialis perennis, Pulmonaria officinalis, Viola mirabilis, Polygonatum multiflorum* and *Geum rivale.* This alliance may also occur in pure *Corylus avellana* woods with no tree layer.

In the areas between the ridges there is mainly a wet deciduous forest vegetation with *Alnus glutinosa* and *Betula pubescens* as dominant trees. The field layer mainly consists of the *Carex riparia* alliance. Differential species of this alliance include *Lysimachia vulgaris, Filipendula ulmaria, Carex riparia, Scutellaria galericulata, Carex remota, Poa palustris,* and *Lycopus europaeus.*

It is most interesting, as stressed by Sjögren (1964, 1974) and Ekstam & Sjögren (1973), and supported by the results of the present work, that several species mainly characteristic of transitional vegetation, such as *Primula veris, Serratula tinctoria, Orchis mascula, Fragaria vesca* and others, are still present in nearly all parts of the forest. Furthermore, species typical of closed forest occasionally grow in the open meadow.

The mosaic structure and the instability of the vegetation on the ridges are common characters. Recolonization by forest is proceeding rapidly on the Litorina ridge, while the Recent ridge offers poor conditions for forest growth. There are *Pinus sylvestris* plantations only on the Ancylus and Recent ridges. There is one *Betula verrucosa* plantation (about 30 years old) on the Litorina ridge. On all ridges there are large areas with only scattered shrubs and trees. In some of the stands investigated there are only single plants of shrubs or trees. There are some pure stands of shrub species such as *Prunus spinosa* or *Juniperus communis.* The wide-crowned *Quercus robur* trees still dominate. The mosaic deciduous forest vegetation of the ridges is rich in transitions between open meadow and closed forest communities, especially on the Ancylus and Litorina ridges.

Review of literature

As already mentioned, floristic studies on Öland started with Linnaeus's famous journey to the island in 1741 (Linnaeus 1745). This visit certainly stimulated the attention of Swedish botanists towards the island's vegetation.

In the first half of the 20th century the vegetation types of Öland were described from ecological and floristic points of view in a large number of publications (e.g. by Danielsson 1918; Sterner 1924, 1926, 1938, 1948, 1955a, b, c, d; Albertson 1940, 1950; Horn af Rantzien 1951).

Phytosociological investigations and work on the productivity and dynamics of vegetation on Öland have been carried out by Sjögren and students working with him (cf. Sjögren 1954a,b, 1961, 1964, 1971, 1974; Rodenborg 1965, 1976, 1977; Ljung 1970; Ekstam & Sjögren 1973; Rosén & Sjögren 1973, 1974; Sjögren et al. 1974).

Vegetation classification in Sweden was discussed in an early work by Nilsson (1902), who divided terrestrial vegetation into units, called "series", corresponding to a type of large-scale ecosystem. Some of these "series" include both wooded and open vegetation. Sjörs (1967) recognized four "series" units of vegetation type: the heath series, comprising plant communities dominated by dwarf shrubs and grasses with dry and narrow "wiry" leaves (e.g. *Deschampsia flexuosa*) together with lichens and mosses; the meadow series, dominated by broad-leaved grasses and lush herbs and mostly without lichens; the steppe series, related to the south-east European steppe, found in Sweden e.g. on limestone cliffs and in the vegetation of the flat limestone heath called "Alvar" on Öland and Gotland (also present in Västergötland, and in Estonia); and, finally, the mire series.

One of the striking features of Swedish vegetation is the marked difference between areas rich in lime ($CaCO_3$) (Trass & Malmer 1973) and areas poor in lime, where the number of species is considerably smaller. The rich flora of the calcareous island of Öland comprises about 1050 species, with about 800 species in the parish of Vickleby (Sterner 1938, 1948).

The poor-rich soil gradient and the relation to the water regime of a stand are often used in a coordinate system for the primary arrangement of the phytocoenoses (cf. Eneroth 1937, Arnborg 1942, Sandberg 1942, Gjærevoll 1956). Horn af Rantzien (1951) placed the emphasis on the water conditions and related factors (i.e. humus content, water storing capacity, depth of soil, ice erosion, flooding and drying out) as factors correlated with the development of amphibious ecosystems in the "Alvar" vegetation on Öland. Rodenborg (1965) distinguished 13 vegetational types in his study in the Albrunna grove on Öland, based, in part, on qualitative observation of the moisture conditions in each type. Rodenborg (1976) also classified vegetation in the Torslunda parish (adjacent to Vickleby) on the basis of land use. He studied successional aspects in dry grassland vegetation in relation to decrease or cessation of grazing. The pioneer vegetation in the shrub layer was dominated by *Juniperus communis, Prunus spinosa* and *Corylus avellana*. The final stage of succession (not yet reached in the area) was thought to be dry deciduous forest dominated by oak.

Four associations within deciduous forests on Öland have been distinguished by Sjögren (1964) and further discussed in two papers (Kielland-Lund 1971; Ekstam & Sjögren 1973), namely: (1) *Ulmo-Fraxinetum* Sjögren n.p. 1971. A *Fraxinus excelsior* - dominated forest type with *Ulmus* spp. *Corylus avellana* in the shrub layer. Differential species are *Mercurialis perennis, Viola mirabilis, Dentaria bulbifera, Pulmonaria officinalis, Polygonatum multiflorum, Geum rivale*. (2) *Betulo-Quercetum melicetosum* Sjögren n.p. 1971. A *Quercus robur-Betula verrucosa* forest type with *Corylus avellana* frequently present in the shrub layer. Differential species are *Poa nemoralis, Melampyrum pratense, Melica nutans, M. uniflora, Veronica chamaedrys, Stellaria holostea, Luzula pilosa*. (3) *Carici elongatae-Alnetum* (*glutinosae*) W. Koch 1925. An *Alnus glutinosa-Betula pubescens* forest type. Differential species are *Carex riparia, Filipendula ulmaria, Caltha palustris, Lysimachia vulgaris, Scutellaria galericulata, Lycopus europaeus*. (4) *Deschampsio-Fagetum* Passarge 1956. A *Quercus robur-Betula verrucosa* low forest type (*Fagus* is not present on Öland) with high frequency of *Juniperus communis* in the shrub layer. Differential species are *Deschampsia flexuosa, Oxalis acetosella, Hypericum perforatum, Veronica officinalis, Luzula campestris, Hieracium pilosella*.

Ekstam & Sjögren discussed (1973) the land use and the vegetation of deciduous forests over the last four centuries in the parish of Vickleby (cf. Study area). All the woods on Öland are intensely influenced by human activities which have affected landscape and vegetation for centuries (cf. Berglund 1969). Thus the presentday vegetation is strongly dynamic. Sjögren (1964, 1974) and Ekstam & Sjögren (1973) stressed the effect of the irregular weather conditions on deciduous forest vegetation on Öland in causing considerable differences in the occurrence of several species from year to year. Field-layer species were found to react and to recover more rapidly than bottom-layer species in response to years of abnormally high or low precipitation. Deciduous forests on Öland were characterized, however, as very heterogeneous, leading to considerable variations in local climatic conditions even within small areas.

Öland is famous for its self-grown grasslands used for

pasture. Studies in the ecology of the semi-natural grasslands have been carried out and are continuing, with the aim of measuring the standing crop during grazing seasons. Recommendations of suitable grazing pressure for conservation of limestone heath vegetation (on the "Alvar") have been made (Rosén & Sjögren 1973, 1974).

Extensive work has been carried out on the distribution of species and ordination of forest and grassland ecosystems in different parts of the world since it became possible to process the information by computer. Most investigators emphasized the gradients of moisture and/or light as major factors determining variation in vegetation composition (cf. Waring & Major 1964; Ayyad & Dix 1964; Wali & Krajina 1973; Wikum & Wali 1974; Bouxin 1975 and 1976).

Studies of microvariations in composition and structure of vegetation as correlated to micro-environmental differences restricted to small areas have proved useful in providing valuable information in the field of plant ecology. Considerable efforts have been made to elucidate vegetation-microenvironmental relationships in forest and grassland ecosystems (cf., for example, MacHattie & McCormack 1961; Lynch 1962; Ayyad & Dix 1964; Gittins 1965; Swan & Dix 1966; Mowbray & Oosting 1968; Wali & Krajina 1973; Wikum & Wali 1974; Bouxin 1976).

Methods and treatment of data

Selection of stands

The choice of size and shape of the stands was difficult, because of the very mosaic and obviously unstable vegetation structure, with several transitional stages between plant communities. The minimal area has no significance when it is not possible to recognize the boundaries of the plant communities. The greatest possible care was taken to avoid subjectivity. It is impossible to eliminate subjectivity completely, but steps could be taken to minimize its effect (Greig-Smith 1964). Therefore, stands were selected in the study area to represent all major variations in composition of vegetation and in environmental conditions. Variations in plant cover were related to the following main conditions:

Light. The shading effect of the wood and of scattered trees and shrubs is very variable in the study area. Measurement of relative light in stands were made, using a simple photoelectric CdS photographic exposure meter (Sextar, Gossen, purchased 1965). Stands could be separated into five groups: (1) open; (2) nearly open; (3) slightly shaded; (4) shaded; (5) closed.

Cover sum percentage of trees and shrubs. Most woody species are of special significance in the study area, particularly in view of their effects on the understory vegetation. The 10 degrees cover-scale, as described below in the section on sampling techniques (see below), was used to sample the tree and shrub layer. The mean cover percentages of all tree or shrub species in each stand were summed to provide a cover sum percentage. The stands were placed in five groups: (1) meadow; (2) meadow with scattered lignoses (transitional); (3) wooded meadow with glades; (4) low cover forest; (5) dense forest.

Moisture gradient. The moisture gradient in the study area can be traced either from the external appearance of the vegetation physiognomy or from the positions of the stands, or from both. In terms of moisture conditions, the stands were characterized as: (1) very dry; (2) dry; (3) dry mesic; (4) mesic; (5) moist. Separation into these five groups was easily done, especially after periods of rain.

Stand position (elevation). The stands are situated in depressions, on the lower, middle or upper parts of slopes, or on level ground. Although slopes are slight (generally $< 2.0°$), there are appreciable differences in vegetation composition and moisture gradient, especially on the Ancylus ridge (Fig. 3). The stands are located only on the highest parts and slopes of the ridges and not between them.

Animal grazing and human interference. The stands were located as far as possible from areas influenced by tourist activities. In 1937, grazing in the west part of the study area suddenly decreased by 70 % and after that cattle grazed almost only on cultivated pastures (cf. Ekstam & Sjögren 1973). However, part of the study area on the Recent ridge was grazed by

Fig. 3. West slope of the Ancylus ridge covered by snow. Scattered *Juniperus communis* shrubs on the upper part of the slope; on the lower part dominance by the deciduous trees *Betula verrucosa* and *Quercus robur*, and the shrub *Corylus avellana*. Wilted *Arrhenatherum pratense* in the foreground. Photo: E. Rosén, March 1976.

cows until the summer of 1975. Stands have therefore been rated as grazed or not.

A total number of 73 stands were randomly distributed, a maximum of 2 km apart, within the parish of Vickleby. They were found to be adequate in including all the variations in conditions mentioned above. In delimiting each stand care was taken to ensure a reasonable microclimatical homogeneity in regard to relative light, shading effect by tree-shrub cover and moisture gradient (see "Variations in microclimatic factors" and Figs. 6 and 7). To be representative, the stands were kept as large as possible, while fulfilling the requirement that they should be reasonably homogeneous. The area of the stands was variable, but not less than 10 x 10 m. Moreover, the numerical values of the coefficients which are used in ordination and classification must be as free as possible from any effect of the stand size (Bouxin 1975). However, all frequency values are inherently dependent on the size of plots, as a result of the species/area curve, which can, moreover, be different in different stands. In a heterogeneous vegetation, the dependence of frequency on plot size is greater than when the vegetation is very homogeneous. Of the 73 stands, 30 were located on the Ancylus ridge, 22 on the Litorina ridge, and 21 on the Recent ridge.

The vegetation analysis for the Ancylus ridge was carried out in the growing season of 1975, that for the Litorina and Recent ridges in 1976.

Sampling of data on vegetation and habitat conditions

The vegetation was stratified into 3 layers: (1) the tree-shrub layer including trees higher than 3 m and shrubs higher than 1/2 m; (2) the field layer, mainly of vascular plants lower than 1/2 m; (3) the bottom layer of bryophytes and lichens. A list of all the species recorded is given in Table 2.

Vegetation sampling techniques

The vegetation in each stand was sampled twice using 1/2 x 1/2 m^2 quadrats to analyse the field and bottom layers, and 2 x 2 m^2 quadrats to analyse the tree-shrub layer. In the stands of the Ancylus ridge 50 plots of 1/2 x 1/2 m^2 were used while 30 were considered adequate to sample the stands on the Litorina and Recent ridges. Fifteen to twenty 2 x 2 m^2 plots were positioned systematically to sample the plants of the tree-shrub layer in each stand.

Greig-Smith (1964) discussed the advantages and disadvantages of random and systematic sampling methods.

A restricted random sampling seemed to be the best solution for this work, taking ease of use in the field into consideration (Ammar 1970; Bouxin 1975). For analysis of the field layer, five equally spaced lines were stretched through the stands and 6–10 random quadrats (1/2 x 1/2 m^2) were placed along each line at positions determined using random numbers.

All the species in each quadrat were recorded and assigned a cover degree according to the following 10 degree cover-scale:

Degree	Range (%)	Mean (%)	Degree	Range (%)	Mean (%)
1	0–10	5	6	51–60	55
2	11–20	15	7	61–70	65
3	21–30	25	8	71–80	75
4	31–40	35	9	81–90	85
5	41–50	45	10	91–100	95

The crown cover of the tree and shrub layer (not the foliage cover, which is less because of the spaces between the leaves) was estimated by its projection over the large quadrats. Litter cover estimates were made in five of the small quadrats, randomly chosen in each stand. The bottom layer species were recorded in the same five small quadrats, as presence or absence in each stand. They were identified by Dr. E. Sjögren.

The number of occurrences of each species (except bottom layer) in the quadrats of each stand was used to calculate its frequency. The mean values of species cover percentages in each stand were calculated by adding the cover values of each species in the quadrats used in the stand and dividing by the number of quadrats. The mean litter cover of the tree species was summed to give a litter cover value sum for a stand. It was noticed that *Quercus robur* litter formed the largest part of the litter cover sum in most of the stands. This may be a result of the comparatively slow decomposition of oak leaves.

Taxonomic nomenclature is according to Lid (1974) for vascular plants and according to Nyholm (1954–69) and Arnell (1956) for bottom layer bryophytes.

Habitat sampling techniques

Light gradient. Of significance to the present work in the consideration of the relative light gradient are the papers by Køie (1951), Sjögren (1961), Waring & Major (1964), Wali & Krajina (1973) and Bråkenhielm (1977). Køie's light gradient is based on four groups, using measurements made out with photosensitive papers; Waring & Major (1964) and Wali & Krajina (1973) used the same method but had six or five groups, respectively, along their gradients. Bråkenhielm (1977) and Sjögren (1961) used a photoelectric cell for their light measurements.

The deciduous forest ecosystem examined here was found to be heterogeneous even within very small areas, except in the forest plantations. Ekstam & Sjögren (1973) and Sjögren (1961, 1964, 1974) discussed the effect of shading on bottom layer species in deciduous forests of Öland.

Because of the rich variation in cover and age of the woods in the study area considerable differencies in exposure cause a great variation of bioclimatic conditions. Measurement of relative light was therefore considered useful for possible correlation with the vegetation of the stands.

Light was measured according to Bråkenhielm (1977). The measurements in a stand were made 50 cm above ground level, using the photoelectric cell with a standard hemispherical diffusor. The meter diffusor was fully shaded by a hand, at a distance of 1 m. The main reason for screening was to minimize the effect of sunflecks (cf. Bråkenhielm 1977). The measurements therefore include only illumination from the sky, with no direct sunlight. Measurements were made in all selected stands during two days of July, 1976, between 10 and 14^h. The sky was clear with no clouds or appreciable haze. The light meter was set at a fixed sensitivity value (e.g. 50 ASA = 18 DIN) and the exposure values ranged from −2 to 24. These exposure values were converted to lux using the table on the back of the meter (5 = 175 Lux; 6 = 250; 9 = 2800 etc.), and percentages were calculated in relation to lux values obtained on an adjacent open field. The open field values were recorded immediately before and after the stand measurements, to avoid possible changes in sensitivity. The measurements were repeated several times depending on the diversity of the light in the stand areas. Only relative values under as similar conditions as possible were required, absolute values being of no significance for comparison. The range of relative light was then classified into 5 categories.

Vegetation moisture index. Many ecological studies have given great attention to variables such as soil depth, water table, soil morphology, topography, and physiographical features in order to classify the vegetation of stands in relation to features related to the moisture gradient. Each of these factors could be shown separately in its simple form, but it is preferable to integrate factors to express the moisture index, as there is no single environmental factor that can fully define the moisture regime (cf. for example Hills 1950; Køie 1951; Whittaker 1960; Loucks 1962; Waring & Major 1964; Ayyad & Dix 1964; Newsome & Dix 1968; Andersson 1970a; Ammar 1970; Wali & Krajina 1973).

For example, Ayyad & Dix (1964), Wikum & Wali (1974) and Ayyad & Ammar (1974) found that stand position (elevation) can be the most decisive feature in expressing moisture regime in a stand. Baines (1973) found considerable differences in a grassland vegetation along the elevation gradient although the slopes were very slight (not more than 1.5°). Whittaker (1956, 1960) derived a moisture gradient based only upon topography. Rowe (1956) mentioned that ecologists who are familiar with the vegetation of a particular region are often able to differentiate the moisture-physiognomy relations of any given community with considerable accuracy. He outlined a simple scheme based upon physiognomy of the undergrowth plants and the moistness of the site. Vegetation as an index of environment (e.g. moisture) is frequently used by European botanists, for example for Öland vegetation (cf. Horn af Rantzien 1951; Sjögren 1961, 1964; Rodenborg 1965, 1976). Goodall (1954) also remarked that the plants themselves serve better as instruments to indicate the complex of environmental conditions than direct measurements of these factors in a site.

In some studies the species themselves have been used to evaluate the water regime. Whittaker (1956) constructed a moisture gradient based upon an average index for the species presented in a stand. Rowe (1956) derived a vegetation moisture index (VMI) which was based directly on the cover-abundance value of the species. Similarly Waring & Major (1964) and Wali & Krajina (1973) calculated their vegetation moisture index and water gradient from available soil moisture and species presence or relative species significance respectively.

Fosberg (1961 and 1967) defined vegetation physiognomy as the external appearance of vegetation, and he stated that the physiognomy of a vegetation is partly a product of gross compositional characteristics such as luxuriance and relative xeromorphy. Becking (1968) concluded: "Thus, lesser vegetation has been recognized as a better environmental indicator than the mature tree layer. Lesser vegetation contains many short-living species which will exhibit greater sensitivity to environmental change than the tree species."

A vegetation moisture index has been suggested in this study derived from a combination of the mean cover values of the field-layer species covering > 1% (five categories) and the stand position (elevation) (four categories). In the species cover scale, a very high cover was rated as five and a very low cover as one. In the elevation scale category one indicates the high position and category four the depression position. Each stand has been assigned to a category of elevation and mean species cover, and an average of the two categories has been taken as the vegetation moisture index. All moisture index values for the 73 stands were then classified into 5 categories.

Meteorological records. In an attempt to compare the local microclimatic conditions on the three ridges in different selected habitats, records of temperature (T°C) and relative humidity (RH%) were made for four weeks in July—August 1977. Two simultaneously recording thermohygrographs (Lambrecht), fitted to record one week at a time, were used continuously. They were placed in standard meteorological screens 1.5 m above the ground, so that T°C and RH% could be measured simultaneously at two different sites. One instrument was at all times in an open meadow site on the Litorina ridge. The second instrument was moved from an open meadow site on the Ancylus ridge, to an open meadow on the Recent ridge, a wooded meadow with glades and a dense cover forest locality on the Litorina ridge. Two visits a day were made to check that the instruments were working accurately. General information about weather conditions, and wind speeds during the period, were recorded.

Mean values of T°C and RH% were calculated for six separate days of each seven day recording period and were based on 24 values taken from the curves, one every hour. Mean maximum and minimum T°C and RH% were also calculated for 6-day periods.

Soil sampling and analysis. Soil samples were collected from three separate positions in each stand. A 40 cm deep hole was dug. Two differently coloured horizons were distinguished (Fig. 4). The first horizon (H_0) was grey to dark grey, about 5 cm deep in the Recent ridge, but about 15—20 cm in both the Ancylus and Litorina ridges. The horizon below (H_1) was greyish-yellow. The soil depth was determined by using a solid long thin iron needle. The needle was pushed down at several positions in each stand down to the first gravelly layer. The depth of soil was measured to the nearest centimetre, but down to a depth of 50 cm only, and the average value calculated. The three soil samples from each horizon of each stand were mixed together. In one stand, on the Ancylus ridge, only the H_0-horizon was considered. Soil samples were taken to the Ecological Station on Öland shortly after sampling, air-dried, packed and transported to Uppsala for analysis. The soil was sampled from the Ancylus ridge stands in August 1975, and from the Litorina and Recent ridges in August 1976.

Fig. 4. Soil profile on the Ancylus ridge (from W-E) showing two differently coloured soil horizons. The surface (upper) horizon (H_0) is grey to dark grey, extending down to 15—20 cm; the horizon below (H_1) is greyish-yellow, extending down to at least 40 cm. In the background is dense deciduous forest with high frequency and cover of *Corylus avellana*. In the open site codominant species are *Festuca ovina, Agrostis tenuis* and *Galium verum*. Photo: F. Hellström, Sept. 1975.

Air-dried soil samples were weighed and passed through a 2 mm sieve in order to separate the gravel and stone fraction which dominated in most of the Recent ridge samples. The weight of this fraction in each stand was determined and expressed as a percentage of the total weight of the soil sample. The portion finer than 2 mm was kept for other physical and chemical determinations.

Soil texture was determined by the Bouyoucos hydrometer method (Bouyoucos 1951). Percentages of sand, silt and clay were calculated. Fractions of sand were separated by the dry sieving method, in which 100 g air-dry soil sample was sieved through a column of three successive sieves of 0.6, 0.2 and 0.063 mm square hole mesh width, by shaking in Pascall shaking apparatus for 0.5 h, to separate coarse, medium and fine sand. Water holding capacity (W.H.C.) was determined by use of the "Hilgard cup method" (Piper 1944). Conductivity (Cond.) as micromhos per cm and pH were determined for the same sample (proportion soil-distilled water 1:2). The samples were shaken for 2 h and left overnight at 20°C. Conductivity was measured in the soil extracts by a Normameter RI model no. 1802 GBID/E conductivity meter, and pH was determined with a glass electrode pH-meter.

Organic matter (O.M.) was determined by the loss-on-ignition method, at 550–600°C for 0.5 h. The loss will then include CO_2 given off from carbonates if present. A simple Passon-model calcimeter (Johansson 1968) was used to determine the $CaCO_3$ content.

Total bound nitrogen (N_{tot}) was determined according to Kjeldahl. The sample was digested with conc. H_2SO_4, with addition of K_2SO_4 and $CuSO_4$. The ammonia formed was distilled off with NaOH solution and collected in boric acid. The nitrogen content of the sample was then determined by back-titration with hydrochloric acid (cf. Nordic Committee on Food Analysis 1976). Determination of titratable acidity (T.A.), cation exchange capacity (C.E.C.) and total exchangeable bases (T.E.B.) for the cations Na^+, K^+, Mg^{2+} and Ca^{2+} was according to methods described by Nömmik (1974). Cation exchange capacity (C.E.C.) is = titratable acidity (T.A.) + total exchangeable bases (T.E.B.).

These methods were proposed for determining T.A. and T.E.B. by extracting the soil with a solution of 1 M NH_4Cl + 0.1 M imidazole buffered at pH 7.0. The procedure was rapid and accurate compared with the reference methods, regardless of soil type and/or base status (cf. Nömmik 1974). Because of the time-consuming nature of the work, the N_{tot} content, T.A., C.E.C., and T.E.B. were determined at the Statens Lantbrukskemiska Laboratorium, SLL) at Ultuna, Uppsala. Because of the high cost the number of soil samples for the C.E.C., T.A. and T.E.B. analysis was reduced.

Hygroscopic moisture (H.M.) was determined by oven-drying the air-dry samples. All physical and chemical measurements were expressed as percentages of the oven-dry weights.

Multivariate analyses

Codification. The recorded frequencies of the field layer species were used only to construct the ordination and classification programs. As the large number of the floristic variables (208) was more than the capacity of the program ORDINA used, only the most frequent species, with > 5 % of presence on one of the ridges or on the three ridges together, were considered (cf. Table 2). The computation was carried out for the same number of species in both programs. The computation was made with two digits, so that species with 100 % of frequency were taken as having 99 %.

Ordination technique. One of the main objects of this study was to make a quantitative assessment of the relationships between the vegetation composition on the shore ridges and important environmental factors.

For the examination of interstand relationships, principal component analysis (PCA) serves the purpose of placing stands relative to each other. These relative positions reflect the compositional relationships between the stands, so that those placed close to each other have a high degree of phytosociological resemblance, and vice versa. The rapid development of computers has made PCA practicable as well as simple ordination techniques like those introduced by Bray & Curtis (1957), Orlóci (1966) and van der Maarel (1969), for example. PCA was introduced in plant ecology by Goodall (1954) and has since been frequently applied (cf. for example Dagnelie 1960; van Groenewoud 1965; Orlóci 1966, 1973; Yarranton 1967a,b,c; Austin 1968; Austin & Greig-Smith 1968; van der Maarel 1969; Barkham & Norris 1970; Jeglum et al. 1971; Walker & Wehrhahn 1971; Wikum & Wali 1974; Bouxin 1975, 1976; Feoli-

Chiapella & Feoli 1977; Feoli 1977; Nichols 1977; Kvillner 1978).

Plant distributions are really syndromes of environmental factors. Stand ordination is therefore often valuable ecologically, as the identification of trends in the ordination is carried out by plotting species values or environmental data on the ordination diagrams. Thus the main axes are related to habitat factors, as has been observed by Bray & Curtis (1957), Ayyad & Dix (1964), Gittins (1965), Austin & Orlóci (1966), Swan & Dix (1966), Greig-Smith et al. (1967), Austin (1968), Austin & Greig-Smith (1968), Kershaw (1968), Bunce (1968), van der Maarel (1969), Chandapillai (1970), Onyekwelu (1972), Whittaker (1972), Ayyad (1973, 1976), Ayyad & Ammar (1974), Bouxin (1975, 1976), Walker (1975), Peet & Loucks (1977), and others.

Classification technique. Goodall (1973) asserts that the choice between the application of ordination or classification is a matter of taste and depends on the intended use of the results. Whittaker (1972) said that the two techniques can be appropriately applied to the same data, but classification is preferable when the vegetation of the study area is very heterogeneous. Similarly, Pielou (1969) suggested that the choice between the two approaches depends on the size of the study area: ". . . whether to classify or to ordinate is a matter of much controversy". Greig-Smith (1964) also asserted that the two approaches are theoretically different but in practice the differences are not so pronounced as they may seem. Bouxin (1975) considered that the choice of technique depends on the aims of the work, the nature of the data, and the capacity and cost of the computers.

In recent years, numerical classification techniques have been widely and effectively used to study vegetation structure, for example by Gimingham et al. (1966), Crawford & Wishart (1966, 1967), Orlóci (1967), Webb et al. (1967), Walker (1968), Mueggler & Harris (1969), Schmelz & Lindsey (1970), Lloyd (1972), Grigal & Ohmann (1975), Ayyad (1976), Ayyad & El-Ghonemy (1976), Moral & Deardorff (1976), Kortekaas et al. (1976), and Eijsink et al. (1978).

The procedure applied in the classification of the stands studied was a numerical agglomerative method, CLUSTAN package (Wishart 1969a,b). The results were analysed in terms of vegetation groups.

Characteristics of the programs used. The computation was made by using ORDINA and HIERAR programs. These programs are accessible on disc via IBM 370/158 computer of the University of Nijmegen, the Netherlands.

(a) The ORDINA program was written by Roskam (1972) on the basis of the PCA method described by Orlóci (1966). The program prints the matrix of dissimilarities between stands (Euclidean distance), the coordinates of the observation vectors (= principal components), the extracted variance percentages per dimension and the diagrams with the position of the stands in a multidimensional space. Five dimensions were extracted and corresponding diagrams were printed by computer for the stands of each ridge and for the three ridges together.

(b) The HIERAR program is a method of the CLUSTAN 1 program developed and described by Wishart (1969 a, b). It is a numerical agglomerative method.

At the beginning of this program, each stand is considered to be a single element cluster. At each fusion step, the two most similar clusters are joined. The analysis terminates when the initial clusters have been agglomerated into a single cluster universe. The entire fusion process can be represented by a dendrogram or a "linkage tree". Each stand is situated at the end of a branch of the diagram. Each fusion is defined by connecting two branches of the diagram. The connections should be drawn by hand parallel to a similarity scale. Details of the hierarchal process used for the HIERAR program can be studied in Ward (1963), Lance & Williams (1967) and Wishart (1969 c).

Four dendrograms were drawn to classify the stands of each ridge and of the three ridges together.

Significance tests for data treatments

Analysis of variance (F-test) for groups with unequal replications was carried out to assess the significant variations in every soil factor along the gradient of the stands of the three ridges. The least significant difference test (LSD-test) was then applied to evaluate the significant difference between the means of pairs of ridges in terms of each soil factor. The significance of the difference between the means of soil factors of the two horizons (H_0 and H_1) was tested by t-test, for equal or unequal sizes. Coefficient of vari-

Fig. 5a. Position of permanent open and dry harvest plot (10 x 10 m) on level ground on the Ancylus ridge. Codominant species are e.g. *Festuca ovina, Agrostis tenuis, Thymus serpyllum, Veronica spicata, Galium verum* and *Arrhenaterum pratense*. In the background on and below the W slope is dense deciduous forest dominated by *Quercus robur* and *Corylus avellana*. Photo: F. Hellström, Sept. 1975.

Fig. 5b. Position of permanent open and dry harvest plot (10 x 10 m) on level ground on the Recent ridge. Codominant species are e.g. *Festuca ovina, Hypericum perforatum, Agrostis tenuis, Galium verum, Poa angustifolia* and *Hieracium pilosella*. Scattered shrubs of *Rosa* spp. and *Juniperus communis*. Photo: F. Hellström, Sept. 1975.

Fig. 5c. Position of permanent open and dry harvest plot (10 x 10 m) on level ground on the Litorina ridge. Codominant species are e.g. *Geranium sanguineum, Helianthemum nummularium, Filipendula vulgaris, Luzula campestris, Festuca rubra* and *Festuca ovina*. In the background dense deciduous forest dominated by *Corylus avellana* and *Betula verrucosa*. Photo: F. Hellström, Sept. 1975.

Fig. 5d. Position of permanent harvest plot (10 x 10 m) in low-cover dry-mesic forest on level ground on the Litorina ridge; in the tree-shrub layer *Quercus robur* is dominant and codominant species in the field layer are e.g. *Deschampsia flexuosa, Melica nutans, Stellaria holostea, Agrostis tenuis, Veronica chamaedrys* and *Convallaria majalis*. Photo: F. Hellström, Sept. 1975.

ations (CV) was used to compare the amount of variation in each soil factor.

Simple correlation coefficients (r) between soil characters at the two horizons, relative light percentages and tree-shrub cover sum percentages and the loading of each stand on the first two ordination components (axes) were used to explain the nature of these axes. Similarly, Chi-square tests (χ^2) were carried out to evaluate the degree of association between the five moisture categories and the five equal segments of the first two ordination axes.

All the statistical methods used here are as described by Sokal & Rholf (1969).

Changes in vegetation

Recent changes in vegetation in deciduous forests of Öland, including the study area, were investigated between 1955 and 1971 by Sjögren (cf. Ekstam & Sjögren 1973; Sjögren 1974). Therefore, in this study, most attention was given to the changes in vegetation in the meadows and forest plantations. Less attention was given to the seasonal variations of the vegetation.

An attempt was made to follow the vegetation dynamics in open meadows and forest plantations for a period of three years from 1975 to 1977. Sixteen permanent sample plots (1 x 1 m^2) were selected along the three ridges to represent local variation in meadows and in forest plantations. The occurrence of each species was recorded twice a year, at the end of May or beginning of June and in mid August. A ten degree cover scale (see "Vegetation sampling techniques") was used to record the cover degree of each species of the field layer. Bottom-layer species were recorded as present or absent. The phenological stages of the field-layer species were recorded as follows: No sign = seedlings, o = vegetative, * = flowering, • = fruiting, – = seeds dispersed and = = wilted and dry. The degree of vigour was also rated, to help in categorization.

Standing crop

Investigations of standing crop of vegetation on the ridges aimed at showing production during the different periods of the growing seasons in 1975, 1976 and 1977.

Four homogeneous permanent sampling plots (10 x 10 m) were used for this study (Fig. 5). Three open and dry meadow plots, one on each ridge, were selected as similar as possible, with the aim of comparing the results for the different ridges. The fourth plot was on the Litorina ridge, in low cover forest of a *Quercus robur* stand.

Five sub-quadrats (1 x 1 m^2) were distributed randomly within each plot and harvested according to the following scheme:

Year	no. of sub-quadrats
1975	1, 2, 3, 4, 5
1976	1, – 3, – – 6, 7, 8
1977	1, 2, – – – 6, – – 9, 10.

Within each sub-quadrat were chosen 6 small (25 x 25 cm^2) quadrats to be used for production studies.

One of the small quadrats was harvested each month between May and October. Plants were clipped about 1 cm above soil surface. The crop was packed in plastic bags and sorted into three categories: dead plants, living herbs, and grasses. The material was dried for 24 hours (at 100°C) after sand, fragments of mosses and lichens had been removed.

Variation gradients

Variations in vegetation composition

It was essential to summarize the large amount of data from vegetation analysis in a readily appraisable form (Table 2) to show the major pattern of vegetation composition on the shore ridges. The following information is available from this table. The total number of species recorded in all three layers is 265, with 213, 176 and 142 spp. on the Ancylus, Litorina and Recent ridge, respectively. In the tree-shrub layer, *Quercus robur, Corylus avellana, Betula verrucosa* and *Juniperus communis* occur in > 25 % of the stands in the study area. These important species are at their greatest frequency on the Litorina ridge, where they occur in > 45 % of the stands. Other very frequent species in the tree-shrub layer are *Sorbus aucuparia, Ribes alpinum, Rosa* spp., *Fraxinus excelsior* and *Prunus spinosa*. These were recorded mainly as shrubs. On the other hand, *Pinus sylvestris* has its highest maximum and mean cover percentage (12.2 %) and occurred in 27 % of the stands on the Ancylus ridge. *Alnus glutinosa* and *Salix cinerea* are infrequent. The total number of tree-shrub species on the Recent ridge is relatively low.

Field-layer species are numerous. *Galium verum, Campanula rotundifolia, Poa angustifolia, Agrostis tenuis, Veronica chamaedrys* and *Achillea millefolium* are important species. These species were recorded in at least 70 % of the 73 stands sampled in the study but are not equally important along the three ridges. *Anthoxanthum odoratum, Phleum phleoides, Anemone pratensis, Allium vineale, Arrhenatherum pratense, Knautia arvensis, Hypericum perforatum, Dactylis glomerata, Festuca rubra, Fraxinus excelsior, Prunus spinosa* and *Fragaria vesca* are at their most frequent, present in > 50 % of the stands, on the Ancylus ridge. *Festuca ovina, Luzula campestris, Plantago lanceolata, Rumex acetosa, Hieracium pilosella, Potentilla tabernaemontani, Silene nutans, Rumex acetosella, Veronica spicata, Thymus serpyllum, Stellaria graminea, Trifolium campestre, Viscaria vulgaris, Sedum acre, Lotus corniculatus, Armeria maritima, Cerastium brachypetalum* and *Dianthus deltoides* are also among the most frequent species, but have maximum presence on the Recent ridge, where they are found in > 50 % of the stands. Species with maximum presence on the Litorina ridge, and recorded in > 50 % of the stands there, are *Deschampsia flexuosa, Viola riviniana, Melampyrum pratense, Quercus robur, Convallaria majalis, Stellaria holostea, Hepatica nobilis, Melica nutans, Luzula pilosa, Lathyrus montanus* and *Anemone nemorosa*. Some species are confined to only one ridge. Of these species present in > 15 % of the stands on the Ancylus ridge are *Moehringia trinervia, Roegneria canina, Melampyrum cristatum, Euonymus europaeus* and *Chamaenerion angustifolium*; on the Recent ridge they are *Carex arenaria, Hypochoeris radicata, Sedum maximum, Plantago maritima* and *Puccinellia distans*; and on the Litorina ridge they are *Viola hirta, Dentaria bulbifera, Anemone ranunculoides, Melica uniflora* and *Viburnum opulus*.

The bottom layer (cf. Table 2) has the largest number of species on the Ancylus ridge (30 out of a total of 37 bottom layer species), while only 18 species were recorded on the Litorina ridge. *Mnium affine* is the most important species. It attains > 50 % presence in total but is not equally important on the three ridges. It is more frequent on the Litorina and Ancylus ridges than on the Recent ridge. Important species, present in > 25 % of all stands, are *Dicranum scoparium, Pleurozium schreberi, Rhytidiadelphus squarrosus, Brachythecium albicans, Brachythecium rutabulum* and *Hypnum cupressiforme*. The following species have a maximum presence on different ridges, namely: *Rhodobryum roseum, Cirriphyllum piliferum* and *Brachythecium velutinum* on the Ancylus ridge, *Abietinella abietina, Cladonia* sp., *Hylocomium splendens, Cirriphyllum piliferum, Polytrichum juniperinum, Climacium dendroides* f. *dep.* and *Tortula ruralis* on the Recent ridge. Each has a maximum presence of > 15 % on at least one ridge. All other bottom-layer species are less frequent.

None of the species can be considered as a major dominant of the whole study area. However, certain species are locally dominant and are distinctly more important in a particular group of stands on each ridge. This feature has been illustrated in the differentiation of vegetation groups, shown in Tables 9 a–c.

Variations in microclimatic factors

Microclimatic data for the three ridges are presented in Table 3, which shows the very wide range of variation within the study area. The average tree-shrub cover sum, for example, was calculated as 68.7 % for the Litorina ridge, 39.8 % for the Ancylus ridge, and 11.3 % for the Recent ridge. These figures give the overall impression of the presence of a sheltering tree-shrub layer on the ridges. However, there are large and frequent local variations in the tree-shrub cover sum on the Ancylus ridge. Some stands are dominated by tree-shrub species giving cover sums of > 10 %: no. 7, 10, 25 and 26 with deciduous tree-shrub species; no. 11 with shrubs of *Prunus spinosa*; no. 14, 15, 16, 17, 19, 23 and 24 with *Pinus sylvestris* trees (plantations mixed with deciduous tree-shrub species); no. 20 with *Juniperus communis* shrubs. Other stands on the Ancylus ridge have no tree-shrub species or have a very low tree-shrub cover sum. Most of the stands on the Litorina ridge have low or dense cover of deciduous tree-shrub species, except no. 1. On the other hand, on the Recent ridge only no. 3, 4 and 18 have cover sums of the tree-shrub layer of > 45 %, no. 3, 4 with *Pinus sylvestris* trees, and no. 18 with mixed *Pinus sylvestris* and deciduous tree species; in no. 6, 7, 13 and 16 there are mainly *Juniperus communis* and *Rosa* spp. with low or very low cover sums (cf. Figs. 6, 7).

Vegetation moisture index categories show some correlation with the density of the tree-shrub layer and with the supply of light reaching the ground. The first two categories (1, 2) of moisture index are frequent among the stands of the Ancylus and Recent ridges, while the third and fourth categories of moisture index are frequent on the Litorina ridge. The intermediate category (3) seems to be relatively more frequent in the Ancylus stands than in the Recent ridge stands. Only one stand (no. 7), on the Litorina ridge, has the highest moisture index (5).

Relative light values, as correlated with the tree-

Fig. 6a. Open and very dry meadow stand (No. 5) on the Ancylus ridge. Codominant species are e.g. *Festuca ovina, Sedum acre, Veronica spicata, Arrhenatherum pratense, Galium verum* and *Phleum phleoides*. Scattered *Juniperus communis* shrubs; in the lower part of the W slope is a deciduous forest of e.g. *Betula verrucosa, Quercus robur* and *Corylus avellana*. Photo: F. Hellström, Sept. 1975.

Fig. 6b. Open and dry meadow stand (No. 2) on the Ancylus ridge. Codominant species are e.g. *Galium verum, Arrhenaterum pratense, Calluna vulgaris, Phleum phleoides* and *Poa angustifolia*. Photo: M. Ammar, July 1976.

Fig. 6c. Open and dry meadow stand (No. 1) on the Recent ridge. Codominant species are e.g. *Festuca ovina, Hypericum perforatum, Agrostis tenuis, Poa angustifolia, Galium verum, Hieracium pilosella* and *Achillea millefolium*. Scattered shrubs of *Juniperus communis*. Photo: M. Ammar, July 1976.

Fig. 6d. Wooded meadow with low cover of *Quercus robur* and position of the dry-mesic stand No. 12 on the Litorina ridge. Codominant field layer species are e.g. *Stellaria holostea, Convallaria majalis, Melica nutans, Veronica chamaedrys* and *Trifolium medium*. Photo: M. Ammar, Sept. 1976.

Fig. 6e. Shaded, dry-mesic meadow stand (No. 13) on the Ancylus ridge. Codominant species are e.g. *Poa angustifolia, Veronica chamaedrys, Anthriscus sylvestris, Dactylis glomerata, Stellaria holostea*, and *Festuca rubra*. To the right (E) scattered trees of *Quercus robur* and *Sorbus aucuparia*; in the lower part of the slope to the left (W) *Betula verrucosa* grows at the edge of the forest. Photo: F. Hellström, Sept. 1975.

Fig. 6f. Low cover (tree-shrub layer shaded) dry-mesic stand (No. 17) on the Litorina ridge. In the tree-shrub layer *Quercus robur* and *Corylus avellana* are dominant. Codominant field layer species are e.g. *Aegopodium podagraria, Pteridium aquilinum, Anemone nemorosa, Hepatica nobilis, Melampyrum pratense, Convallaria majalis* and *Stellaria holostea*. Photo: M. Ammar, July 1977.

Fig. 7a. *Pinus sylvestris* plantation with frequent presence of *Sorbus aucuparia* and *Fraxinus excelsior*; position of mesic stand No. 18, on the Ancylus ridge. Codominant species in the field layer are e.g. *Rubus caesius, Rubus idaeus, Poa nemoralis, Stellaria holostea, Convallaria majalis* and *Sorbus aucuparia*. Photo: F. Hellström, Sept. 1975.

Fig. 7c. Dense, mesic deciduous forest ; positon of stand No. 26 on the Ancylus ridge. *Betula verrucosa* and *Corylus avellana* are dominant trees. Codomiant species in the field layer are e.g. *Convallaria majalis, Hepatica nobilis, Melampyrum pratense, Oxalis acetosella, Rubus saxatilis* and *Viola riviniana*. Photo: F. Hellström, Sept. 1975.

Fig. 7b. Dense, mesic deciduous forest; position of stand No. 7 on the Ancylus ridge. In the tree-shrub layer e.g. *Betula verrucosa* and *Quercus robur* are dominant. Codominant species in the field layer are e.g. *Melampyrum pratense, Rubus saxatilis, Convallaria majalis, Hepatica nobilis* and *Anemone nemorosa*. Photo: F. Hellström, Sept. 1975.

Fig. 7d. Dense, mesic deciduous forest; position of stand No. 18 on the Litorina ridge. In the tree-shrub layer *Corylus avellana* and *Quercus robur* are dominant. Codominant species in the field layer are e.g. *Melica uniflora, Anemone nemorosa, Hepatica nobilis, Mercurialis perennis, Dentaria bulbifera*. Photo: M. Ammar, July 1976.

shrub cover sum, give a rough idea of the pattern of stratification of vegetation in each stand. A more precise impression of variation in light supply may be obtained from the figures of the range of variation or of standard deviation (SD) in a stand. Some of the forest stands show a wide range of variation in the light distribution, for example no. 11, 14, 17 and 18 (Ancylus), no. 2, 11, 12, 14, 19, 20, 21 and 22 (Litorina) and no. 3, 4 and 18 (Recent). The same wide range of variation can be measured within stands with few or scattered tree-shrub species, such as no. 9, 21, 29 and 30 (Ancylus) and no. 6, 7, 13 and 16 (Recent). Nevertheless, the understory species pattern was fairly homogeneous within the stands studied. It is also apparent that some stands without tree-shrub species do not attain the maximum (100 %) relative light values, for example no. 1, 8, 27 and 28 (Ancylus) and no. 1, 2, 17, 19, 20 and 21 (Recent), as they are close to forest margins. This reduction of light is also typical of the transitional stands on the Ancylus ridge.

Variations in soil characters

The results of the soil analyses are presented in the Tables 4a, b and c. A general idea about the magnitude of variation of the soil parameters in the stands may be obtained from the range and coefficient of variation (CV). Most of the characters have a very wide range of variation while others have a narrow range. Narrow ranges of variation between the surface horizon, H_0, and the horizon below, H_1, are shown by pH, sand particles and the medium sand fraction. Values for most soil characters decrease considerably with depth, except for pH values and for the coarse texture fractions, such as particles > 2 mm, total sand particles, and the coarse sand fraction, which have higher values in H_1 than in H_0. Results of texture analyses show that all stands are sandy with average percentages ranging from 88.7–93.1 % sand in H_0 and from 92.9–95.6 % in H_1. The medium sand fraction has the highest percentage (> 50 %) of the various sand fractions. The average percentages of particles > 2 mm have a wide range, with 2.5 for the Ancylus ridge, 12.5 for the Litorina ridge and 67.7 for the Recent ridge.

The percentage of clay is very low (average not higher than 2.3 %) but the total percentage of silt and clay may be correlated with other soil characters, for example in stand no. 7 (Ancylus), no. 20 (Litorina) and no. 17 (Recent). The percentages of silt + clay are maximum in these stands, at least in H_0; consequently most other soil characters also have maximum values.

Soils in the study area are more acidic in H_0 than in H_1. The range of all mean pH values is 4.7–5.4. pH-values of H_0 are gradually lower from the Ancylus towards the Recent ridge. Some of the transitional stands on the Ancylus ridge have high pH values, for example no. 27, 28 and 29. $CaCO_3$ was present only in stand no. 17 (Recent) with 0.3 and 0.2 % in H_0 and H_1. On the other hand, Ca^{2+} has the highest values of the cations: in H_1 from 1.29 meq./100 g (Ancylus) to 4.24 meq./100 g (Litorina); in H_0 from 4.63 meq./100 g (Ancylus) to 7.12 meq./100 g (Recent).

Soil depth differs considerably between the three ridges and gradually decreases from the Ancylus towards the Recent ridge. One striking feature is that on the Recent ridge some stands with shallow soil and with high content of stone-gravel material (particles > 2 mm) also have high soil parameter values. These may even be higher than in some stands of dense cover deciduous forest (Litorina, Ancylus), e.g. in the open stands no. 1, 11, 15, 19 and 21 (Recent) and no. 5 (Ancylus). On the other hand, some open stands, no. 5, 8 and 9 (Recent), have low soil parameter values in spite of having relatively deep soil and a relatively low content of particles > 2 mm. These features may be explained by the fact that the volume of shallow soils with a high stone-gravel content is small and consequently the root systems are highly concentrated. The level of the water table is also gradually relatively higher towards the sea, from the Ancylus to the Recent ridge. However, the soil water parameters were not useful either in the comparison between the stands or as a meaningful moisture level indicator. Waring & Major (1964) and Wali & Krajina (1973) solved a similar problem by using a correction formula to calculate the available moisture from the field moisture content by correction for bulk density, stoniness and water contents of stones. Other chemical properties such as organic matter, total nitrogen, conductivity, and amounts of cations show a similar pattern, having high values in some of the forest stands but also in most open stands (Recent). Values generally increase gradually from the Ancylus towards the Recent ridge.

A precise assessment of these soil variations may also be achieved by examining the results in Tables 5 and 6. Table 5 shows the vertical variation in various soil characters within the stands. The mean values for each soil character in all stands of each ridge are given for each of the two horizons H_0 and H_1. All characters show a definite pattern with depth. It is apparent that variations with depth in all characters are statistically significant at least on one ridge, except for pH and the coarse sand fraction, which do not vary significantly. Most soil characters show highly significant variations with depth on the Ancylus and Recent ridges. Water holding capacity, total nitrogen, conductivity, K^+, Na^+, Mg^{2+}, and clay are the only characters which vary significantly with depth on the Litorina ridge. The variations of soil characters in the two horizons of the ridges are shown in Table 6, which gives the mean values for each soil character for the two horizons in all stands of the ridges recorded.

Soil characters show a definite pattern and vary significantly between the ridges; values are generally higher in H_0 than in H_1. Soil texture shows highly significant variations between the ridges in both horizons, except for the medium sand and clay fractions in H_0. Particles > 2 mm (stones + gravel material) and pH show highly significant variation in both horizons between the ridges. K^+ varies significantly between the ridges in both horizons, and Na^+ in H_1; but the other cations show no significant variations between the ridges. Soil water characters are clearly associated with chemical characters such as O.M., N_{tot} and conductivity. However, soil water and these interrelated factors show highly significant variation between the ridges only in H_1. Moreover, although values of hygroscopic moisture and titratable acidity do not vary significantly between the ridges, the variation between the means of pairs of ridges is significant.

In conclusion, these results emphasize that there are some environmental differences between the geologically separated shore ridge systems. There are large differences in edaphic conditions depending on soil volume and depth and drainage on the different ridges.

Variations in local climate

The vegetation of the study area depends to a large extent on local climatic conditions. Variations in the local climate on the three ridges are shown in Fig. 8 and Table 7. The figures in the table show that during the first two weeks of the field recordings weather conditions were abnormal, e.g. the precipitation (45 mm) exceeded the normal July total for Öland, and the mean temperature was lower than usual. Differences between the sites during the first two weeks are therefore not pronounced, especially in respect of temperature.

Relative humidity (RH) shows only slight differences, for example mean RH in two corresponding open sites was slightly higher on the Litorina than on the Recent ridge, and also slightly higher in the glade site on the Litorina ridge. During the second two weeks, there were distinctly higher temperatures and low precipitation. The recorded temperatures were lower, and the RH-values higher in the open site on the Litorina ridge than in the corresponding open site on the Recent ridge. Temperatures were considerably higher, and RH-values lower at the open Litorina ridge site than at the dense forest site nearby.

Relatively low wind velocities were recorded at the Litorina ridge sites while the wind velocity ranges were wider both on the Ancylus and Recent ridges; the highest values were on the Ancylus ridge. Wind velocity decreased sharply from open sites to the dense deciduous forest site; this decrease ranged from 44.4 % to 52.2 % for two nearby stands on the Litorina ridge. The Litorina ridge generally had lower temperatures and wind velocities and higher RH values than the other ridges.

Local climatic conditions were therefore shown to differ between the ridges and to fluctuate considerably within short periods of time. There are also considerable differences in local climate between different vegetational types on the same ridge.

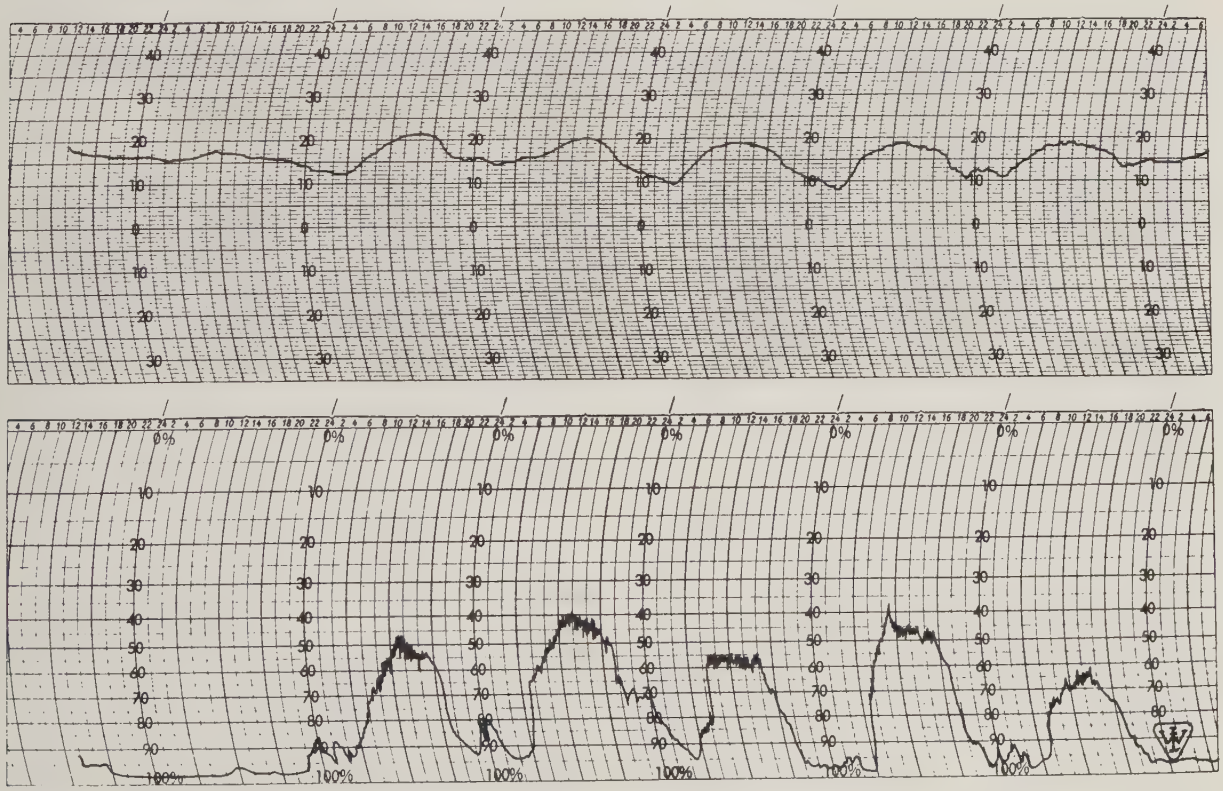
Distribution of species in relation to light and moisture

Relating composition of vegetation to categories of environmental factors is a major interest of phytosociologists. Each factor can be taken separately or a group of interrelated factors may be synthesized and

Fig. 8a. Seven-day records of temperature (above) and relative humidity (below), 27 July–2 August 1977. Site: open dry meadow on the Litorina ridge. Simultaneous with Fig. 8b.

8b. Seven-day records of temperature (above) and relative humidity (below), 27 July–2 August 1977. Site: open dry meadow on the Recent ridge.

8c. Seven-day records of temperature (above) and relative humidity (below), 3—10 August 1977. Site: open dry meadow on the Litorina ridge (identical with that on Fig. 8a). Simultaneous with Fig. 8d.



8d. Seven-day records of temperature (above) and relative humidity (below), 3—10 August 1977. Site: closed deciduous forest on the Litorina ridge.

used in the form of an environmental index. Categories of factors or indices can be determined either objectively using quantitative data or by subjective judgement. Both approaches have been used in this section of the paper, with the aim of illustrating different distribution patterns of important species in the field layer in relation to the gradients in relative light and moisture index. The species distribution has been indicated by the average cover values in stands referred to particular categories. The five categories of relative light are: (1) 6–24 %, (2) 25–42 %, (3) 43–60 %, (4) 61–78 % and (5) 79–100 %. The moisture categories (see above) are: (1) very dry, (2) dry, (3) dry mesic, (4) mesic, and (5) moist (Table 8). Table 8 shows the very pronounced variations of the species cover along the light and moisture index gradients. The field-layer species exhibit a clear pattern along these gradients. The distribution patterns of the species along the relative light and moisture gradients are mirror images of each other. Some species are concentrated at category no. 5 of light and category no. 1 of moisture index, where they are highly dominant, becoming rather less dominant, or gradually sparse or absent, in other categories. Such species are: *Veronica spicata, Thymus serpyllum, Hieracium pilosella, Sedum acre, Artemisia campestris, Helianthemum nummularium, Potentilla tabernaemontani, Carex caryophyllea* and *Ranunculus bulbosus.*

Other species are concentrated at category no. 1 of light and category no. 5 (4) of moisture index. Their cover in the study area tends to decrease gradually or they may become absent altogether from other categories. Such species include *Dentaria bulbifera, Oxalis acetosella, Luzula pilosa, Convallaria majalis, Lathyrus montanus, Mercurialis perennis, Maianthemum bifolium, Hepatica nobilis* and *Anemone nemorosa.* Other species attain their highest cover value in intermediate categories, for example, *Agrostis tenuis, Anthoxanthum odoratum, Anthriscus sylvestris, Deschampsia flexuosa, Fragaria vesca, Poa angustifolia, Festuca rubra, Dactylis glomerata, Rumex acetosa, Veronica chamaedrys, Melica nutans* and *Laserpitium latifolium.* Few species are indifferent to these gradients. The distribution pattern of all species is related to the tree-shrub layer in their behavioural cover sum values in the same way as to the light gradient.

The distribution of several field layer species along the gradients of light and moisture clearly indicated that there is no overall homogeneous habitat in the study area. Thus detailed studies of the differentiation of vegetation including the frequent transitions between communities are essential for the description of the plant cover on the shore ridge systems.

Phytosociological relationships

Classification of vegetation

The observation that the vegetation of the study area is highly heterogeneous suggested the possibility of dividing it into different vegetational groups. For this purpose agglomerative classifications were applied. To facilitate understanding of possible community relations, four dendrograms (Figs. 9 and 10) were constructed, one for the stands of each ridge and one for all the stands, based upon similarity of vegetation of the stands. If the 24 % level of similarity is arbitrarily chosen as a dividing point, these dendrograms separate into four (Litorina), three (Ancylus and total stands) and two (Recent) groups. Most of these groups can be divided into subgroups. The distinctiveness of the groups and subgroups also becomes apparent in the comparison with the average environmental parameters and with the average occurrence of the common species (Tables 9 a–c).

Ancylus ridge

The dendrogram in Fig. 9a shows three major clusters of related stands: A, open meadow stands (left); B, slightly shaded dry mesic transitional stands (centre); and C, mesic to dry mesic stands in both deciduous and coniferous forests (right). The vegetation group A can be classified into two subgroups, A_2 and A_1, comprising the stands at very dry and dry moisture levels, respectively. Similarly the vegetation group C can be divided into two subgroups C_2 and C_1, with *Pinus sylvestris* plantation stands and dense deciduous forest stands, respectively.

Variations in the distribution pattern of the common species and in environmental factors acting on different vegetation groups are remarkable (Table 9a). From this table, it can be seen that *Galium verum* (> 94 % frequency) is a highly frequent species in the stands of group A and its subgroups. *Festuca ovina, Arrhenatherum pratense, Phleum phleoides, Mnium affine, Abietinella abietina* and *Rhytidiadelphus squarrosus* are species with a somewhat lower frequency (> 50 % of mean occurrence value) in the stands of the group A.

The stands of subgroup A_2 have high frequencies of *Veronica spicata, Festuca ovina, Campanula rotundifolia, Potentilla tabernaemontani, Thymus serpyllum, Hieracium pilosella, Sedum acre, Arrhenatherum pratense, Phleum phleoides, Abietinella abietina, Rhytidiadelphus squarrosus,* and *Mnium affine. Artemisia campestris* and *Saxifraga granulata* are important only in this subgroup. *Arrhenatherum pratense, Phleum phleoides, Calluna vulgaris, Poa angustifolia, Veronica chamaedrys, Brachythecium albicans, Rhodobryum roseum, Mnium affine* and *Pleurozium schreberi* (> 40 % of the mean occurrence value) are highly frequent in the stands of subgroup A_1.

The transitional group B has several species in common with the fairly distinct groups A and C. *Prunus spinosa* as a shrub reaches the highest dominance in the tree-shrub layer of group B (10.5 % mean cover value). *Veronica chamaedrys, Agrostis tenuis, Poa angustifolia, Galium verum, Melampyrum pratense, Prunus spinosa, Arrhenatherum pubescens, Achillea millefolium, Mnium affine, Rhytidiadelphus squarrosus, Brachythecium velutinum, Cirriphyllum piliferum* and *Brachythecium rutabulum* are frequent species in group B (> 35 % of the mean occurrence value).

Vegetation group C is codominated by *Corylus avellana* and *Pinus sylvestris* in the tree-shrub layer (> 20 % mean cover value). *Quercus robur, Betula verrucosa* and *Sorbus aucuparia* (> 10 % mean cover value) are less dominant in group C. *Hepatica nobilis, Melampyrum pratense, Convallaria majalis, Viola riviniana, Fraxinus excelsior, Stellaria holostea, Pleurozium schreberi* and *Brachythecium rutabulum* (> 30 % mean occurrence value) are highly frequent species in the field and bottom layers. The tree-shrub layer in subgroup C_2 is overwhelmingly dominated by *Pinus sylvestris* (45.8 % mean cover value) and *Sorbus aucuparia* (10 % cover value). The important species in the field and bottom

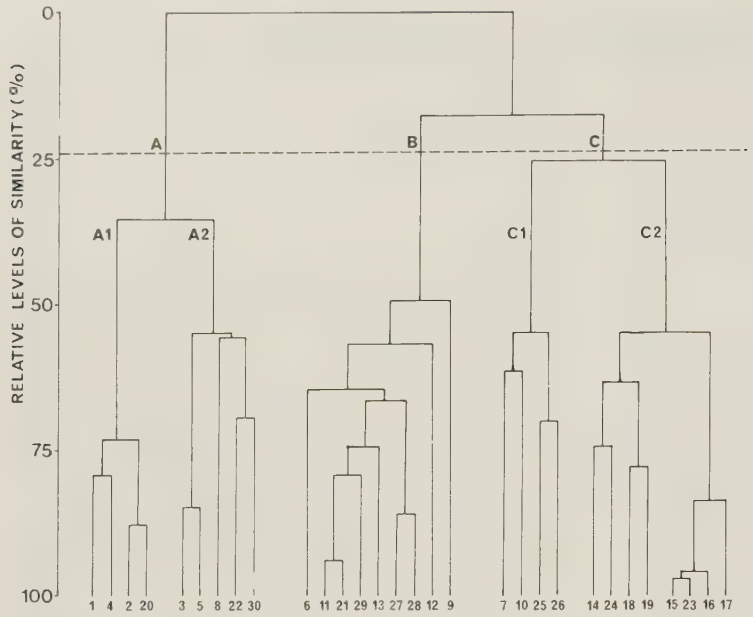
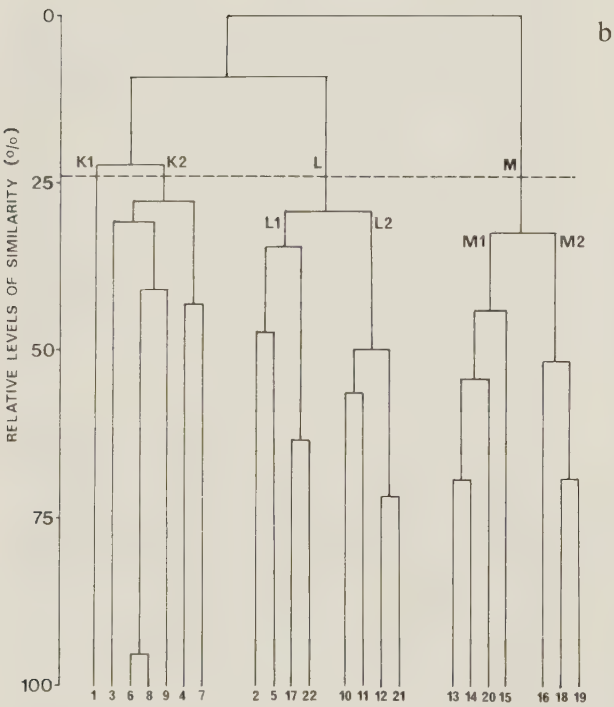
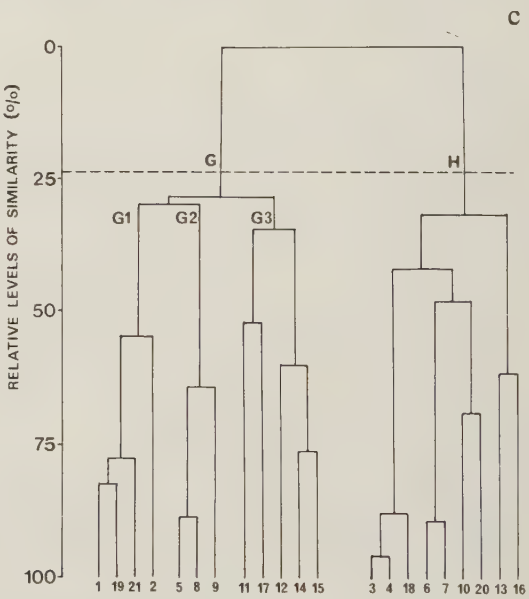


Fig. 9 (a–c). Ancylus, Litorina, and Recent ridge stands: Dendrograms obtained by application of the agglomerative classification technique. At a 24 % similarity level (dashed line) the dendrograms yield three, four, and two groups, respectively.





layers of C_2 are *Anthoxanthum odoratum, Arrhenatherum elatius, Agrostis tenuis, Poa angustifolia, Poa nemoralis, Fraxinus excelsior, Stellaria holostea, Pleurozium schreberi* and *Brachythecium rutabulum* (> 20 % mean occurrence value). In contrast, the tree-shrub layer in subgroup C_1 is dominated by *Corylus avellana* (40 % mean cover value), while *Quercus robur* and *Betula verrucosa* are less dominant species (with 20 % and 21.3 % cover values, respectively). In the field and bottom layers of C_1 the frequencies of *Hepatica nobilis, Melampyrum pratense, Convallaria majalis, Viola riviniana, Fraxinus excelsior, Oxalis acetosella, Mnium affine* and *Brachythecium rutabulum* are about equally high (> 40 % mean occurrence value).

An obvious feature of the pattern of the understory species in Table 9a is the frequent presence in A (top of table) of a large group of species which are insignificant in C, while the reverse is true of another group of species (bottom of table). However, these groups are connected through the stands of group B.

The variations in environmental characters of different vegetation groups are very pronounced and show a definite pattern. Relative light is at its maximum, > 90 %, in the stands of group A and gradually decreases towards group C, while the mean tree-shrub cover sum, moisture index categories and mean litter cover sum show increasing values in the direction A to C. The percentage of coarse material (particles > 2 mm, sand and sand fraction) is highest in the stands of group A, and lowest in those of group C, but the highest and lowest presence of fine soil material (fine sand, silt and clay) is the reverse. Soil water values vary with soil texture, with the lower values in the more coarse textured soils. pH has its highest value in group B and its lowest in group C. The other chemical characters follow a different pattern, with the highest values in group C and the lowest in group A.

Litorina ridge

As a result of the agglomerative clustering of stands on the Litorina ridge, the vegetation can be classified into four groups (Fig. 9b). These are K_1 and K_2 at the left of Fig. 9b, with one open stand (no. 1), stands of glades (no. 6, 8), transitional stands (no. 3, 9), and stands of low density in a *Betula verrucosa* plantation (no. 4, 7); the groups L and M contain deciduous forest stands, which are dry mesic (low cover forest) and mesic (dense cover). They are in the centre and at the right of Fig. 9b, respectively. The vegetation groups L and M can each be classified into two subgroups. The stands of group K_2 are slightly heterogeneous. Nevertheless, these stands cluster into one vegetation group, as the relationship between these stands of mixed character is closer than to stands of any other group.

Table 9b represents the variations in the distribution pattern of the common species and in the environmental characters of the different groups. The variations registered have a wide range. *Allium vineale, Helianthemum nummularium, Galium verum, Plantago lanceolata, Luzula campestris, Saxifraga granulata, Dicranum scoparium* and *Mnium affine* are frequent species in group K_1 (> 70 % mean occurrence value). *Achillea millefolium, Galium verum, Poa angustifolia, Calluna vulgaris, Deschampsia flexuosa, Melampyrum pratense, Pleurozium schreberi* and *Dicranum scoparium* (> 30 % mean occurrence value) are frequent species in group K_2. *Juniperus communis* and *Betula verrucosa* are locally dominant in the tree-shrub layer.

The stands of group L are dominated in the tree-shrub layer by *Quercus robur* (mean cover value 46.7 %). *Betula verrucosa* is the next dominant tree in the group (mean cover value 10.7 %). The understory species *Deschampsia flexuosa, Veronica chamaedrys, Melampyrum pratense, Stellaria holostea, Melica nutans, Mnium affine* and *Rhodobryum roseum* reach high frequency (> 50 % mean occurrence value). The subgroup L_2 is overwhelmingly dominated by *Quercus robur* (54.4 % mean cover value) in the tree-shrub layer. *Deschampsia flexuosa, Veronica chamaedrys, Agrostis tenuis, Melampyrum pratense, Stellaria holostea, Melica nutans, Poa angustifolia, Trifolium medium, Convallaria majalis, Mnium affine* and *Rhodobryum roseum* are frequent field- and bottom-layer species (> 40 % mean occurrence value). Subgroup L_1 is also dominated by *Quercus robur* (38.7 % mean cover value) in the tree-shrub layer. *Betula verrucosa* (19.5 % mean cover value) is subdominant. *Melampyrum pratense, Stellaria holostea, Melica nutans, Anemone nemorosa, Deschampsia flexuosa, Veronica chamaedrys, Hepatica nobilis, Viola riviniana, Aegopodium podagraria, Mnium affine, Rhodobryum roseum* and *Brachythecium rutabulum* are frequent species in the understory layers (> 35 % mean occurrence value).

Group M is dominated by *Corylus avellana* and *Quercus robur* (> 43 % mean cover value) in the tree-shrub layer. *Betula verrucosa* (13.7 % mean cover value) is subdominant. *Melampyrum pratense, Stellaria holostea, Anemone nemorosa, Fraxinus excelsior, Hepatica nobilis, Dentaria bulbifera, Convallaria majalis, Viola riviniana, Oxalis acetosella, Mercurialis perennis*, and *Maianthemum bifolium* are frequent species in the understory (> 31 % mean cover value). Subgroup M_1 is dominated by *Corylus avellana* (57.4 % mean cover value) in the tree-shrub layer. *Betula verrucosa* and *Quercus robur* are subdominant (> 22 % mean cover value). The highest frequencies among the understory species are those of *Stellaria holostea, Anemone nemorosa, Fraxinus excelsior, Hepatica nobilis, Convallaria majalis, Viola riviniana* and *Oxalis acetosella.* Subgroup M_2 is overwhelmingly dominated by *Corylus avellana* and *Quercus robur* (60 % mean cover value). High frequencies among the understory species were recorded for *Melampyrum pratense, Stellaria holostea, Anemone nemorosa, Hepatica nobilis, Dentaria bulbifera, Convallaria majalis, Mercurialis perennis, Viola riviniana, Melica uniflora, Oxalis acetosella* and *Maianthemum bifolium* (> 47 % mean occurrence value).

Application of the agglomerative clustering technique has clearly made it possible to classify the stands into different vegetation groups. The members of each pair of groups are in most cases linked together by having at least one of the dominant species in common.

Variations in environmental characters of different vegetational groups (Table 9b) are remarkable. Relative light is at its maximum of 100 % in group K_1 and gradually decreases towards a minimum (12.9 %) in group M. In contrast, moisture index categories, mean tree-shrub cover sum and mean litter cover sum have their highest values in group M and gradually decrease towards group K_1. Some soil characters show a definite trend in the vegetation groups, such as percentage of particles > 2 mm, coarse sand fraction and silt particles. They have their highest values in group K_1 and gradually decrease to the lowest in group M. Percentage of sand varies in the opposite direction. Other soil characters also have their highest values either in group K_1 or group M, but differences are small.

Recent ridge

The dendrogram (Fig. 9c) indicates two major clusters of related stands: open, very dry or dry stands to the left and slightly shaded, dry mesic to mesic stands mainly with *Juniperus communis* and *Calluna vulgaris* to the right. Group G includes a large number of stands, clustered below 50 %. This suggests the possibility of dividing it into three subgroups, G_1, G_2 and G_3. These three subgroups are located in three separated places. Only the stands of G_3 have previously been grazed. There are marked variations in distribution pattern of common species and in environmental characters of the vegetational groups (Table 8c). *Festuca ovina* (> 88 % mean frequency) is a highly frequent species in the stands of group G and its subgroups. *Galium verum, Achillea millefolium, Plantago lanceolata, Rumex acetosella, Dicranum scoparium, Brachythecium albicans* and *Rhytidiadelphus squarrosus* (> 50 % mean occurrence value) are frequent.

In group H, *Pinus sylvestris* (14 % mean cover) was recorded as dominant only in stands no. 3 and 4 but *Juniperus communis* (5.8 % mean cover) is relatively dominant in the tree-shrub layer. High frequencies were also measured for *Deschampsia flexuosa, Calluna vulgaris, Carex arenaria, Galium verum, Luzula campestris, Festuca ovina, Dicranum scoparium, Mnium affine*, and *Pleurozium schreberi* (> 34 % mean occurrence value). *Hieracium pilosella, Poa angustifolia, Achillea millefolium, Campanula rotundifolia, Rumex acetosa, Hylocomium splendens* and *Hypnum cupressiforme* (> 23 % mean occurrence value) are less frequent species.

The most frequent species in G_1 are *Veronica spicata, Viscaria vulgaris, Sedum acre, Allium vineale, Hieracium pilosella, Agrostis tenuis, Cladonia* sp., *Mnium affine, Abietinella abietina* and *Hypnum cupressiforme*; in G_2 *Carex arenaria, Phleum phleoides, Stellaria graminea, Potentilla tabernaemontani, Sedum acre, Campanula rotundifolia, Armeria maritima, Thymus serpyllum, Ranunculus bulbosus, Anemone pratensis, Trifolium campestre, Pimpinella saxifraga, Cladonia* sp., *Abietinella abietina* and *Hylocomium splendens*; in G_3, *Hieracium pilosella, Thymus serpyllum, Cerastium brachypetalum, Lotus corniculatus, Agrostis tenuis, Luzula campestris, Aira praecox, Hypnum cupressiforme* and *Polytrichum juniperinum.* All these species attain > 40 % of mean occurrence value.

Although each group and subgroup is characterized by its high frequency species, some of the frequent species are the same in each of the pair of groups and in the different subgroups.

Variations in environmental characters of different vegetational groups and subgroups are pronounced (Table 9c). Relative light is almost twice as high in the group G as in group H. It is at its maximum in subgroup G_2. Moisture index level is very dry or dry in the stands of G and its subgroups, except for stand no. 17 which is dry mesic. However, stands of group H are either dry mesic or mesic. Values of mean tree-shrub cover sum and mean litter cover are only moderately high in H.

The soil depth does not vary so much between G and H, but there is some difference in soil depth between the subgroups, as it is greatest in G_2 (26.0 cm) and considerably less in G_1 and G_3. The percentages of particles of sand and of particles > 2 mm are highest in stands of the subgroup G_2; consequently the proportions of silt and clay vary in the opposite direction. The soil water varies with soil texture, with the lowest values in the more sandy soils. pH is at a minimum in group H and a maximum in G_2 and G_3. Conductivity and Ca^{2+} cations are highest in subgroup G_3. Subgroup G_2 has the lowest values of most of the other characters. Values for total exchangeable base and cations of Ca^{2+}, Mg^{2+} and Na^{+} are higher in group G than in H, while other chemical characters vary slightly between the groups.

All ridges

The result of the classification of ridge vegetation includes separation into vegetation groups and subgroups. These groups are related firstly to relative light and secondly to moisture index levels and tree-shrub species layer. Each of the groups and subgroups has certain dominant and highly frequent as well as fairly restricted species. There are only single species which show very high frequencies in the very dry - dry groups. In the dry mesic and mesic groups two or more species are highly frequent. Most of the vegetation groups and subgroups are interrelated, at least on anyone ridge.

The classification work was continued in order to reveal the relations between the vegetation groups or subgroups which are shown by the application of the agglomerative clustering technique to the three ridges together. The possibility of maintaining the boundaries between the vegetation types of the three ridges was examined. So a classification, and subsequently an ordination of all 73 stands studied was applied.

As a result of the agglomerative clustering of all the stands, the vegetation can be classified into three clusters (Fig. 10). Mainly transitional stands cluster (I) at the left; low and dense cover deciduous forest stands cluster (II) in the centre; and open and mainly very dry stands in a compact cluster (III) to the right. Cluster I is split into three major subgroups. In subgroup I_3 are found stands of group H (Recent ridge) mixed with two closely related stands, no. 6 and 8, of group K_2 (Litorina). This subgroup is locally dominated by *Juniperus communis* and *Betula verrucosa* in the tree-shrub layer with *Deschampsia flexuosa, Calluna vulgaris, Pleurozium schreberi* and *Dicranum scoparium* as frequent species. Subgroup I_2 includes subgroup C_2, dominated by *Pinus sylvestris* in the tree-shrub layer (Ancylus) and stand no. 4 (Litorina). This stand is dominated by *Betula verrucosa* in the tree-shrub layer (Ancylus) and stand no. 4 species, as in C_2, are *Arrhenatherum elatius* and *Poa angustifolia, Pleurozium schreberi* and *Brachythecium rutabulum. Anthoxanthum odoratum, Agrostis tenuis, Poa nemoralis, Stellaria holostea* and *Fraxinus excelsior* are frequent in C_2. Subgroup I_1 includes the transitional stands of group B (Ancylus) and also the stands of subgroup A_1 (Ancylus). It also includes the transitional stands no. 3 and 9 of K_2 (Litorina) and the dry mesic open stands no. 10 and 20 (without *Juniperus communis*) of the group H (Recent). *Arrhenatherum pratense, Phleum phleoides, Poa angustifolia, Galium verum, Festuca ovina* and *Mnium affine* are frequent species in this subgroup.

Similarly, cluster II is split into two closely related subgroups: subgroup II_1 consists of stands of mesic dense cover deciduous forest and subgroup II_2 of stands of dry mesic low cover deciduous forest. Subgroup II_1 includes the two most similar subgroups of the Ancylus and Litorina ridges, namely C_1 and M. Subgroup II_2 mainly consists of the stands of group L (Litorina) and stand no. 9 (Ancylus). Stand no. 9 (Ancylus) belongs to the transitional group (B) of the Ancylus ridge but is ranked together with group L (Litorina) which has a very low cover tree-shrub layer and is surrounded by dense forest.

Subgroup II_2 is dominated by *Quercus robur* in the tree-shrub layer, with *Deschampsia flexuosa, Veronica chamaedrys, Melica nutans, Melampyrum pra-*

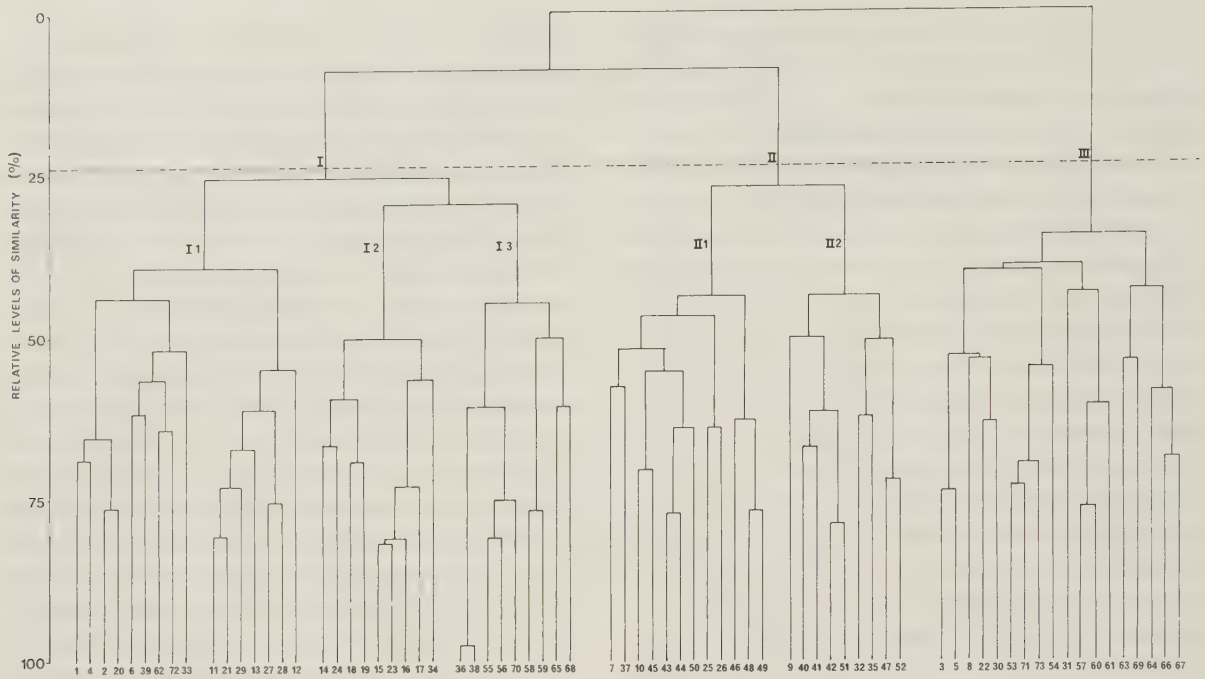


Fig. 10. All stands: Dendrogram obtained by application of the agglomerative classification technique. At a 24 % similarity level (dashed line) the dendrogram yields three groups. Stands: 1—30 Ancylus; 31—52 Litorina; 53—73 Recent ridge.

tense, Stellaria holostea, Mnium affine and *Rhodobryum roseum* as frequent species. Subgroup II_1 on the other hand, represents a more "climax"-like stage in this vegetation, dominated for example by *Corylus avellana* and *Quercus robur* in the tree-shrub layer, with *Oxalis acetosella, Convallaria majalis, Mercurialis perennis, Hepatica nobilis* and *Fraxinus excelsior* as frequent species.

Finally, cluster III includes only the open meadows, mainly the very dry ones. It includes groups G (Recent) and the subgroups K_1 (Litorina), and A_2 (Ancylus). *Galium verum, Festuca ovina, Helianthemum nummularium, Hieracium pilosella, Veronica spicata, Thymus serpyllum, Abietinella abietina* and *Brachythecium albicans* are frequent species.

These results of the study area classification go some way in indicating relationships between certain vegetation groups on the three ridges. The relationships between the deciduous forest stands and also those between stands of the open and very dry groups are closer than between the stands of any other groups. In contrast, the transitional groups show more diffuse clustering and therefore more variety with regard to dominant and frequent species and to environmental factors influencing the stands. The stands of *Pinus sylvestris* (I_2) are related to the transitional group and this reflects the tolerance of some graminaceous species of open dry habitat, which are still frequent in that plantation, together with a large number of deciduous forest shrubs and understory species. The *Pinus sylvestris* group (I_2) is close to the *Juniperus* and *Calluna* group (I_3) probably because of similarly low pH values. The deciduous forest group (II) has an intermediate position between the open and the transitional groups. This reflects the instability of this vegetation, which is still at various stages of development towards a "climax".

Group III is situated at the right of the dendrogram instead of at the left, so that the dendrogram reflects increasing instability from left to right, and not a successional trend.

The results also show that even within the heterogeneous structure of the vegetation of the study area, arbitrarily divided into open meadow groups, transitional groups and forest groups, there is formed a continuum, which can be correlated with gradients in environmental factors. It can be said with confidence

that the classification of the vegetation is related primarily to differences in light, moisture, canopy cover and species composition and secondarily to other interrelated factors, such as soil factors. Accordingly, it is quite appropriate to ordinate these stands.

Phytosociological gradients

The distribution pattern of common species has been represented (Tables 8 and 9a–c) in relation to several environmental gradients, but this may not be completely satisfactory because the gradients were treated separately whereas the phytosociological structure is determined by a combination of factors of quite different character. The composition gradients, which are represented by ordination axes, illustrate multitudes of physical and biotic interacting factors. The distribution of species along these composition gradients can therefore be expected to reflect their relative positions in the ecosystem.

The percentage variation accounted for by each of the five components extracted by PCA, for stands of the individual ridges and the three ridges together, are:

Axis	Variance %			
	A	L	R	ALR
1	31.9	30.2	28.4	29.0
2	14.4	14.9	13.8	9.4
3	9.3	9.6	12.1	6.2
4	5.8	7.2	9.5	5.2
5	4.5	5.8	7.7	4.8

Only the first two axes are considered here and the analysis of additional axes is not warranted because none contains much additional information. The ordination of stands along the first two axes is illustrated in Fig. 11.

The abundance of some of the common species has been plotted on ordination diagrams of the stands, to illustrate some aspects of their phytosociological behaviour.

The distribution patterns of some selected species

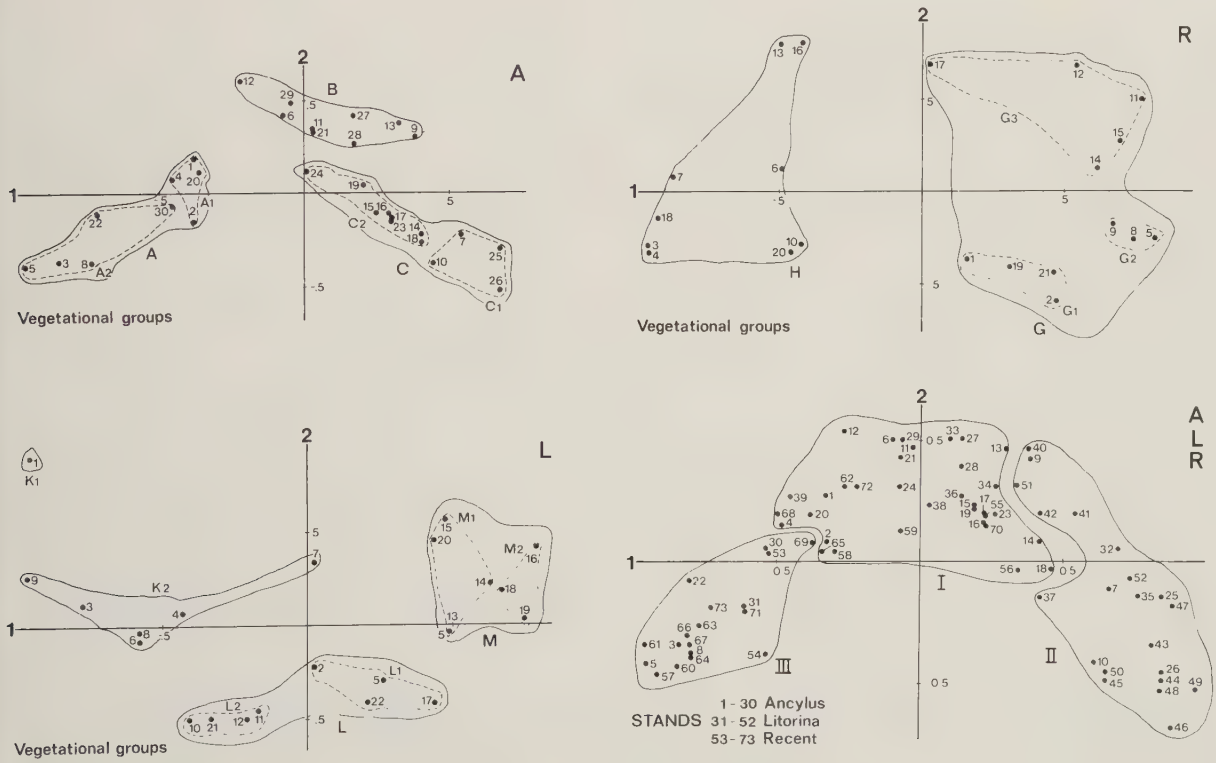
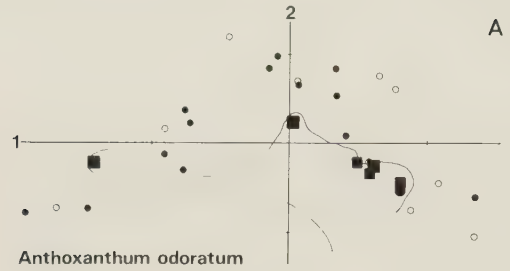
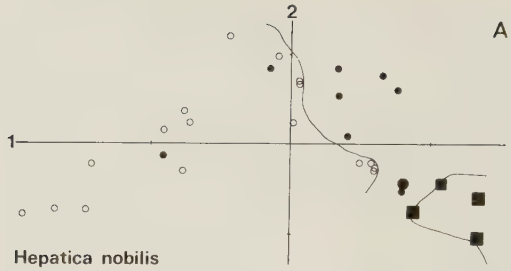


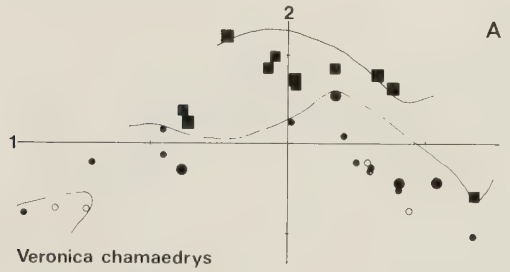
Fig. 11. Distribution of stands in relation to the first two components (axes). Solid and dashed lines encircle stands belonging to the vegetation group and subgroups obtained by application of agglomerative classification technique (Figs. 9 and 10).

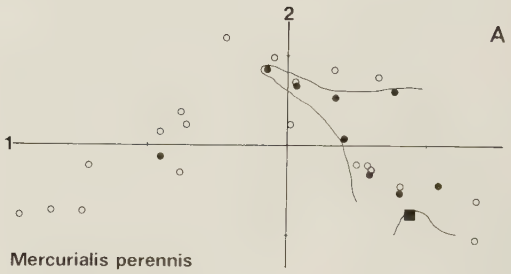
Fig. 12. Distribution of selected tree-shrub species in relation to the first two axes of the stand ordinations of the three ridges. The sizes of the circles, in descending order, represent the following cover percentages: > 80, 61–80, 41–60, 21–40, and < 20. The dots indicate the position of those stands where a species was not recorded.

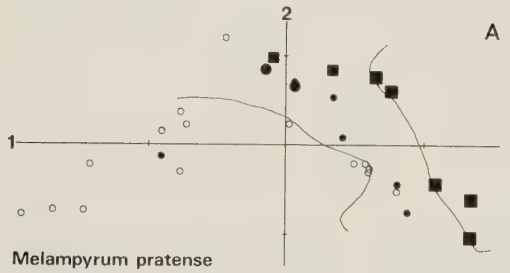
Fig. 13. Distribution of selected field layer species in relation to the first two axes of the stand ordination of the three ridges. Occurrence is shown as percentage of frequency: > 75 (large squares), 51—75 (small squares), 26—50 (large circles), and < 25 (small circles). Open small circles indicate the position of stands in which a species was not recorded. Lines are drawn to separate (with few exceptions) the stands belonging to each symbol. The species of each ridge have been arranged beginning with those with their occurrence centered to open vegetation and finishing with those centered to forest vegetation.

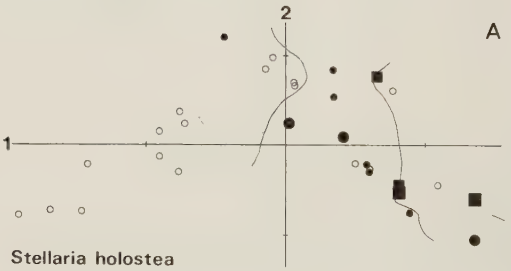


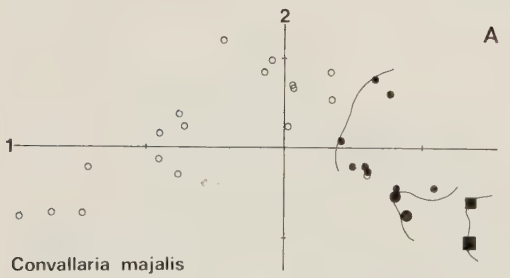


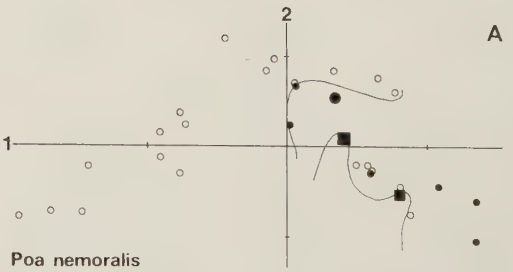












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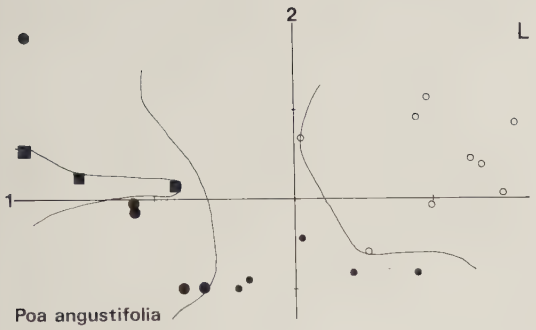

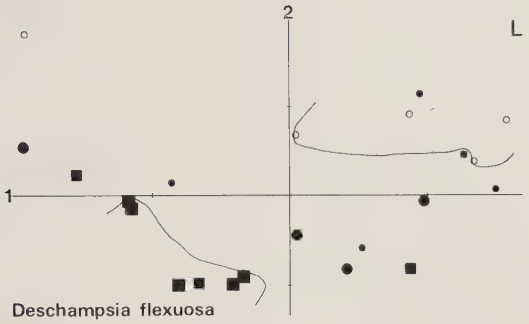

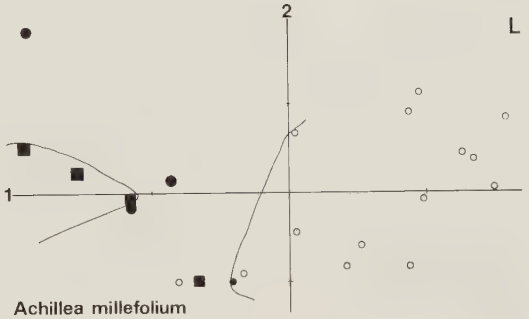

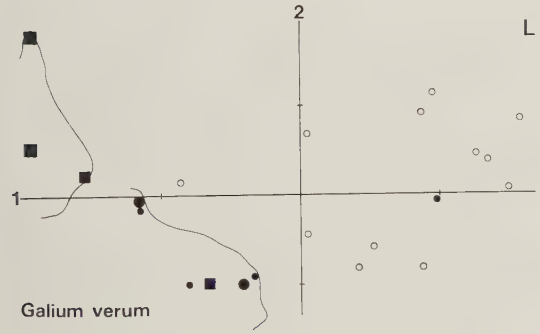

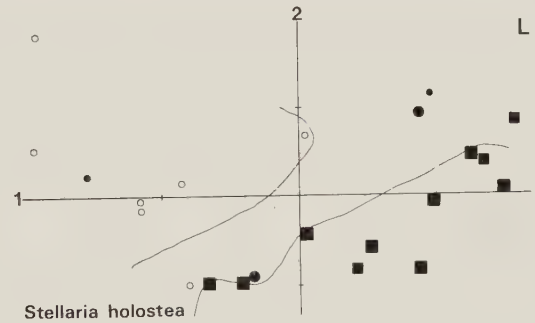

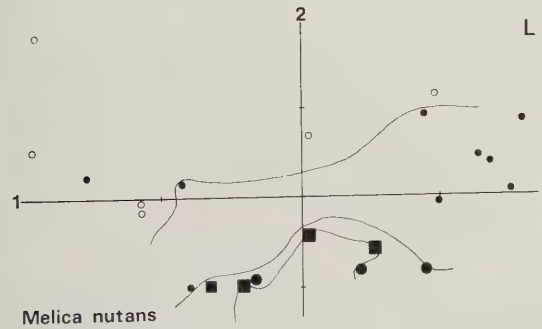

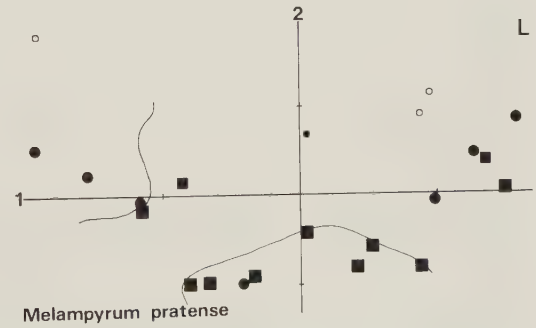

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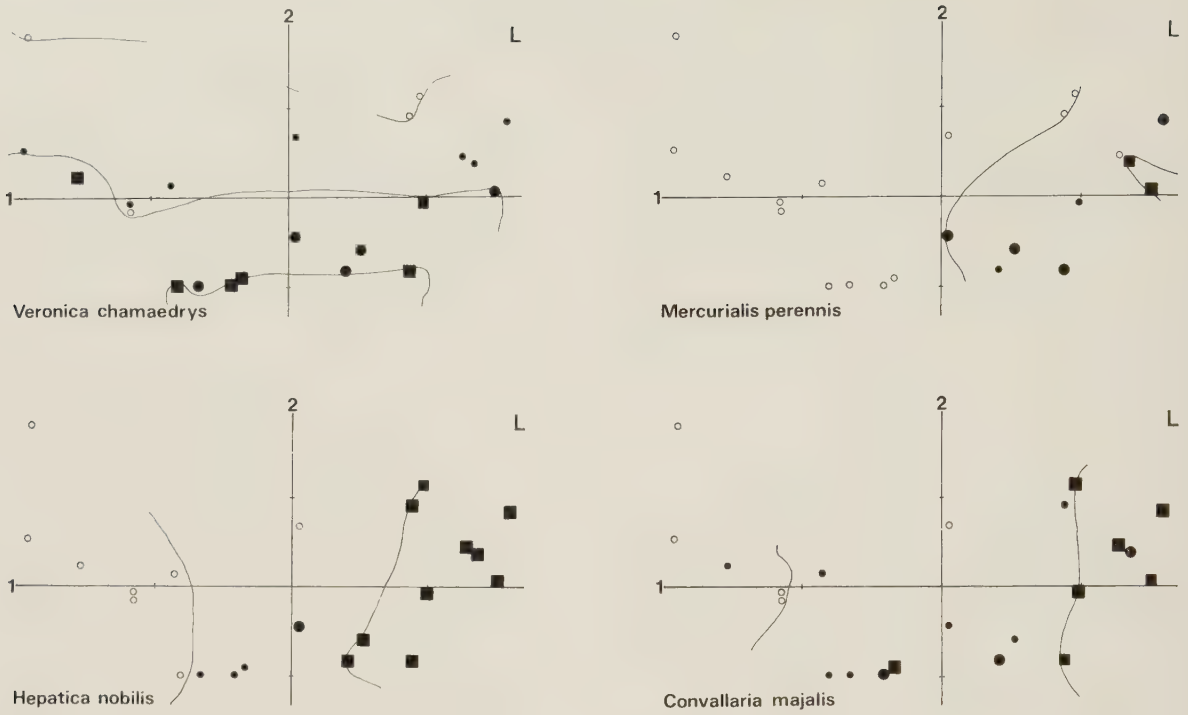


Fig. 13 (continued)

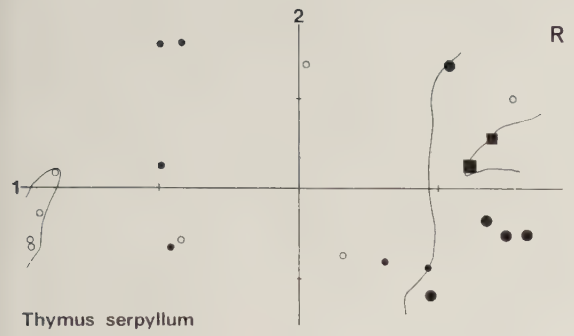
of the tree-shrub layer, as expressed by their cover values, are represented separately in the ordination diagrams (Fig. 12). The percentage cover values are shown by five sizes of circles, representing ranges, > 80, 61—80, 41—60, 21—40, and < 20 %. The small dots indicate stands in which a species was not recorded.

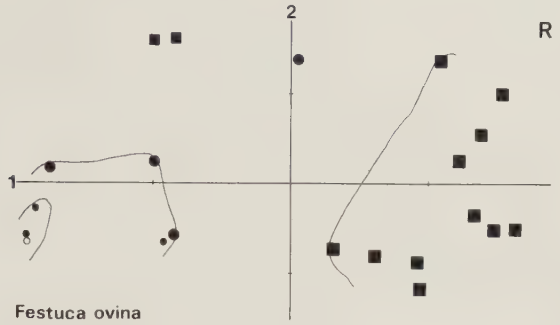
Similarly some common species of the field layer are shown on the ordination diagrams (Fig. 13) by five symbols representing different frequency values, as follows: > 75 (large squares), 51—75 (small squares), 26—50 (large circles) and < 25 (small circles). Open small circles indicate stands in which a species was not recorded. Lines are drawn to separate the stands belonging to each symbol or pair of symbols, to facilitate visual examination of the pattern of the species.

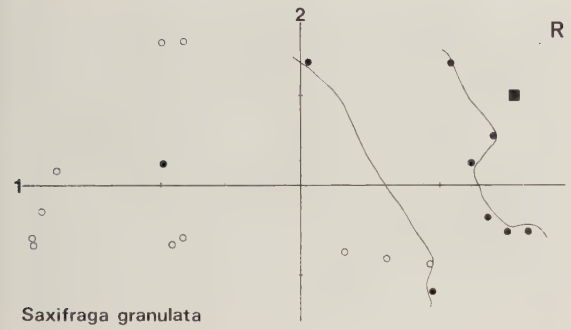
The presence (P) or absence (A) of selected species of the bottom layer are shown in stand ordination diagrams (Fig. 14). Each species is represented by a line type.

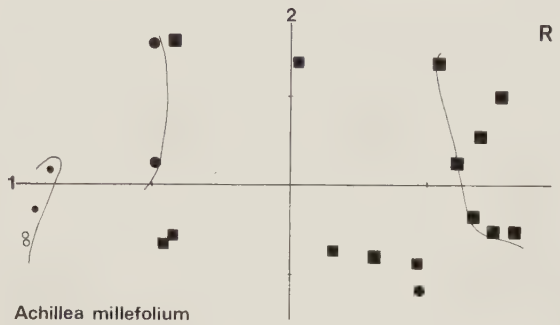
The stand ordination diagrams (Fig. 11) reveal a very clear pattern, with the same segregation of groups and subgroups as was derived from the dendrograms for the ridges.

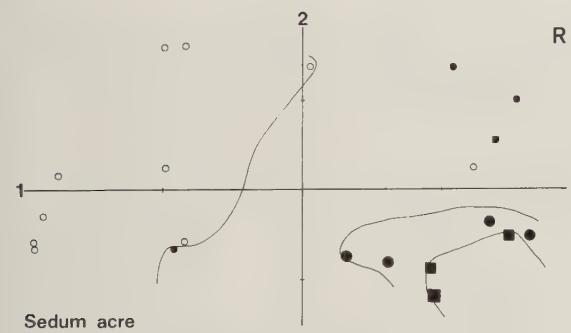
An examination of the pattern of the species in the ordination diagrams (Figs. 12, 13 and 14) suggests that the entire species assemblage represents a vegetational continuum, very clearly differentiated along the first axis but less clearly along the second axis. Thus the first axis lies in the direction of maximum vegetational variations. Some species are restricted to one vegetation group, for example, *Pinus sylvestris* in the tree-shrub layer, *Sedum acre, Saxifraga granulata* and *Artemisia campestris* on the Ancylus ridge, and *Saxifraga granulata, Pleurozium schreberi* and *Abietinella abietina* on the Recent ridge. Other species are present in two or three groups, but most of these show a preference for one vegetation group. A few species may be occasional in some vegetational groups, for example, *Mercurialis perennis, Hepatica nobilis* and *Festuca ovina* on the Ancylus ridge, and *Galium verum* and *Achillea millefolium* on the Litorina ridge. The lack of relationships between the distribution pattern of most common species along the second axis implies that the phytosociological structure of the vegetation of the shore ridges in the study area is associated mainly with one single dominant factor or a dominant group of interrelated factors.

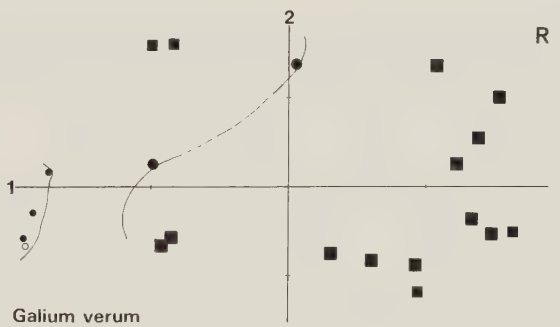


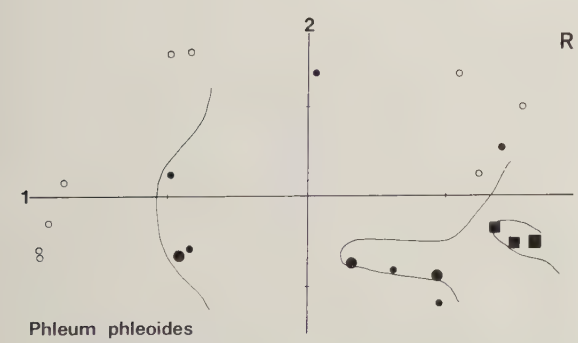












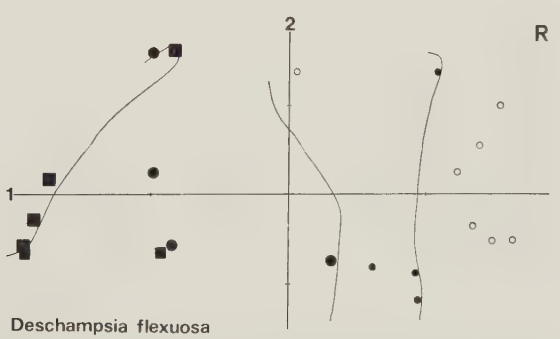


Fig. 13 (continued)

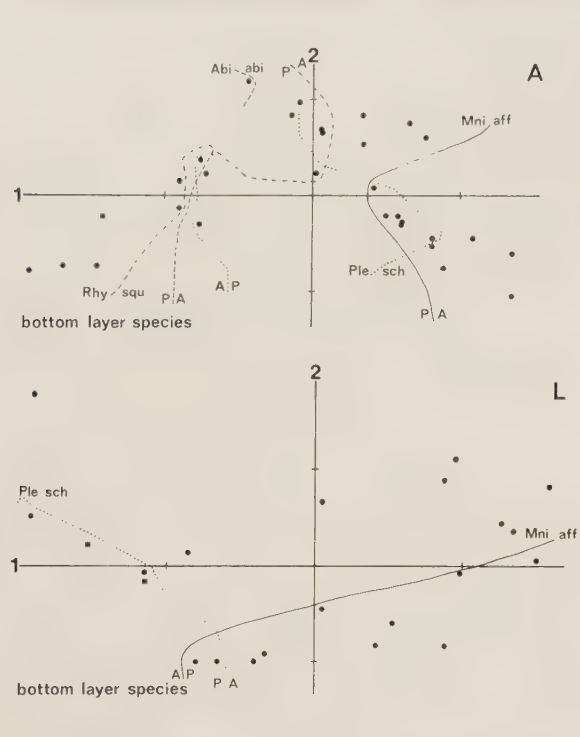


Fig. 14. Distribution of selected bottom layer species in relation to the first two axes of the stand ordinations of the three ridges. The species are represented by different lines to separate the stands in which they were absent (A) or present (P). Abbreviations (Abi abi = *Abietinella abietina*; Bra alb = *Brachythecium albicans*; Dic sc = *Dicranum scoparium*; Hyp cup = *Hypnum cupressiforme*; Mni aff = *Mnium affine*; Ple sch = *Pleurozium schreberi*; Rhy squ = *Rhytidiadelphus squarrosus*).

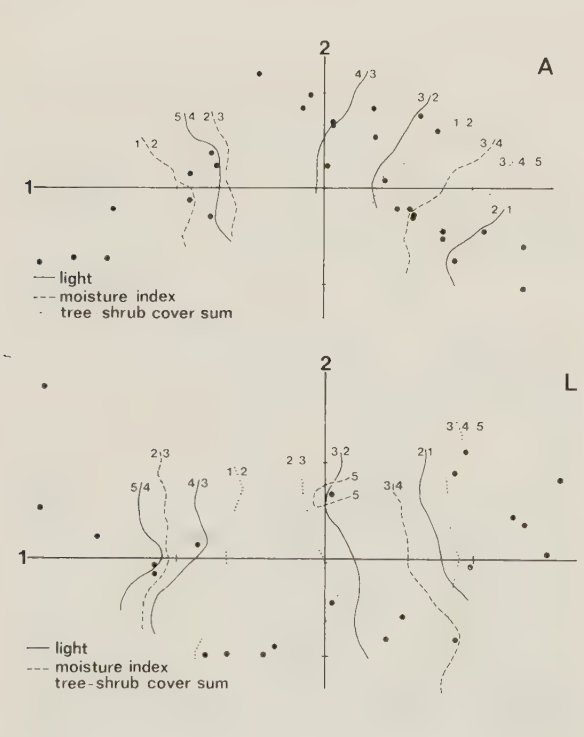


Fig. 15. Distribution of categories of microclimatic factors in relation to the first two axes of the stand ordinations of each ridge and the three ridges together. Categories of relative light percentage: (1) 6–24, (2) 25–42, (3) 43–60, (4) 61–78, and (5) > 78. Categories of tree-shrub cover value sum are arranged similarly: (1) < 29.6, 29.6–59.2, 59.3–88.8, 88.9–118.4, and > 118.5. Vegetation moisture index: (1) very dry, (2) dry, (3) dry-mesic, (4) mesic, and (5) moist conditions. Different lines separate (with few exceptions) the stands belonging to each category.

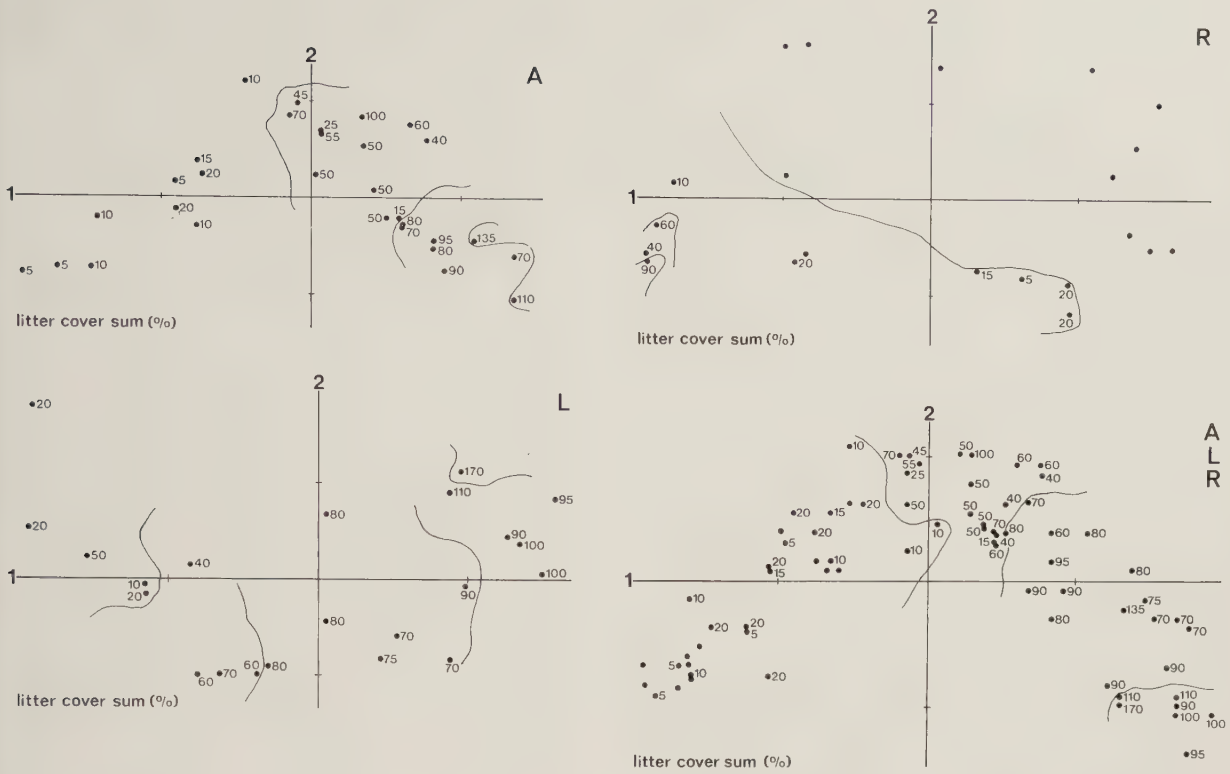


Fig. 16. Distribution of the percentages of litter cover sum from trees and shrubs in relation to the first two axes of the ordination of stands of each ridge and the three ridges together. Lines were drawn to assist in the visual examination of the litter cover pattern. The free dots indicate the position of stands in which litter was not recorded.

The nature of phytosociological gradients in the study area

An attempt has been made to explain the nature of the phytosociological gradients considered in the present study, as represented by the first two ordination axes.

Simple correlation coefficients between the first two axes and several environmental factors, except moisture index, have been calculated (Table 10). A χ^2-test showed a highly significant relationship between the categories of moisture index and five equal segments of the first axis, but there was a significant relationship for the second axis only for Ancylus stands and for the stands of Litorina. Table 10 shows that the correlations are extremely high between light, tree-shrub cover, and litter cover and the first axis. On the other hand, there is a highly significant correlation between tree-shrub cover and the second axis of the Ancylus ridge stands and all stands together. The computations were carried out by using IBM 370/155 at UDAC (Uppsala).

Soil character correlations are mostly low, < 0.50. Significant correlations with the first axis are more numerous than with the second one. Both axes correlate better with soil characters of H_1 rather than H_0. There are more significant correlations with pH than with other soil characters. Some of the relatively high correlations (> 0.50) are those between the first axis and pH of the Recent ridge (both horizons), pH (H_1) of the Ancylus ridge, and of all stands, O.M. (H_0) of the Ancylus ridge and clay particles (H_1) of Recent ridge stands. Highly significant correlations with the second axis are shown only by pH (H_0) of the Ancylus ridge and by the fine sand fraction (both horizons) of all stands.

The relationships between the phytosociological gradients and each of the microclimatic factors are shown in Fig. 15. In this figure, and in all the diagrams discussed below, lines are drawn, with very few

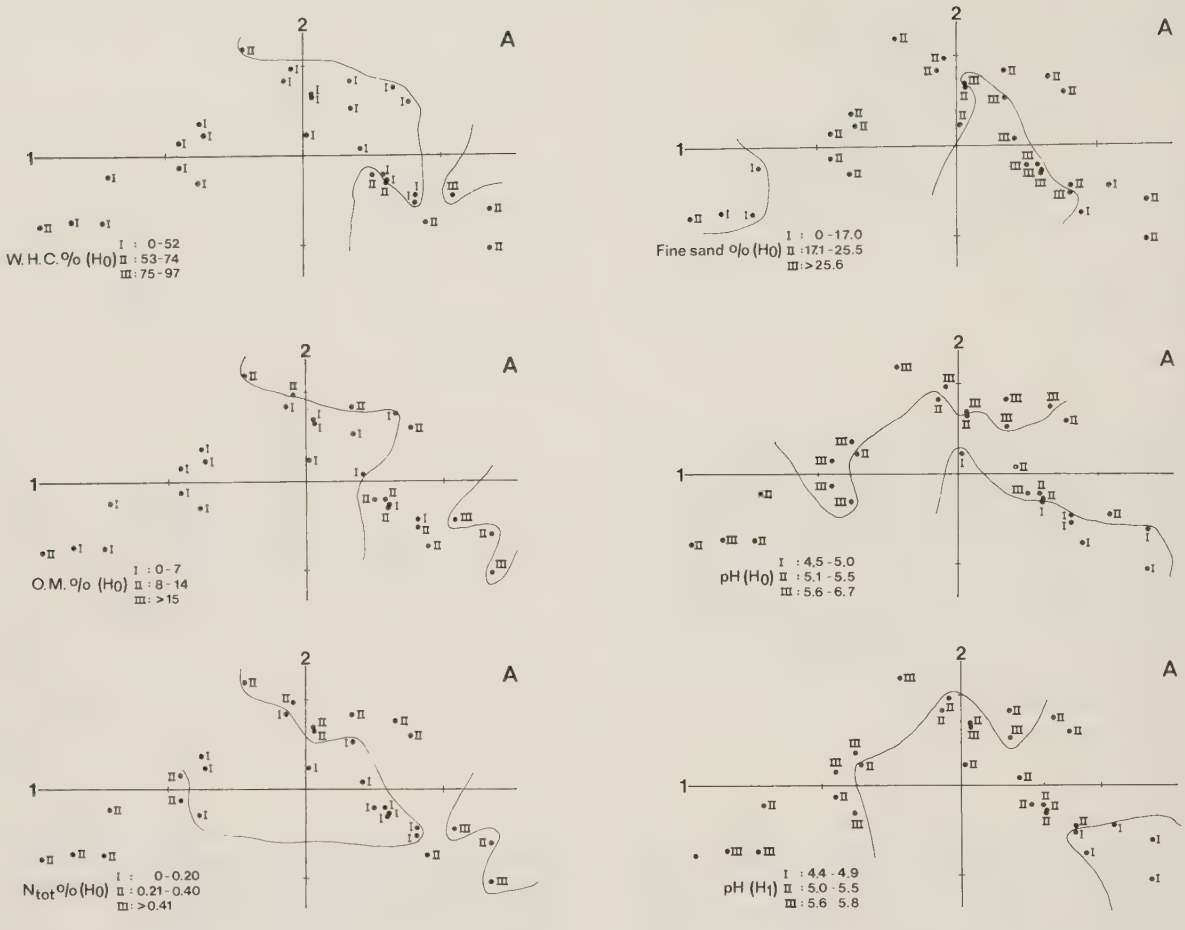
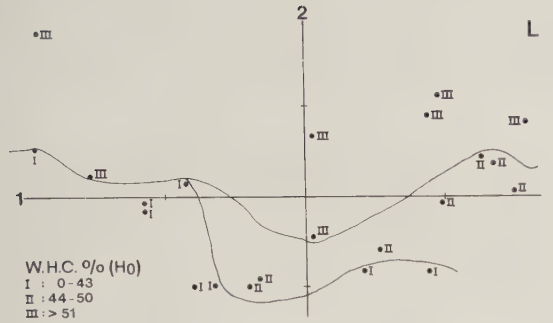
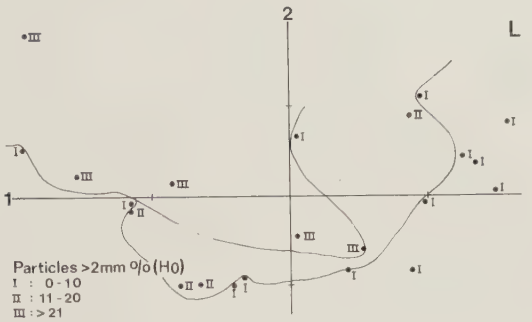


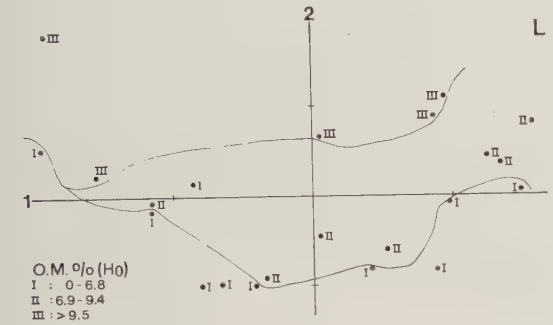
Fig. 17. Distribution of selected soil characters in relation to the first two axes of the ordination of stands of each ridge and the three ridges together. The lines separate (with few exceptions) stands belonging to each category. The range of each category of these characters are given in each diagram.

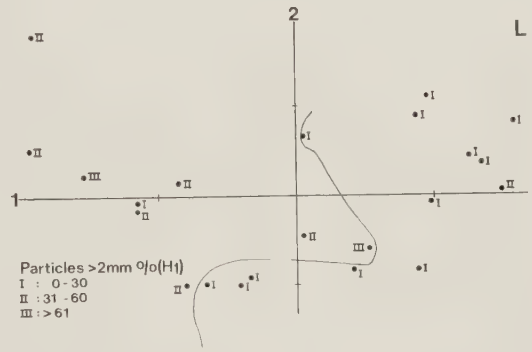
exceptions, to separate the stands belonging to each of the five categories into which these factors are divided. The percentages of relative light are arranged as follows: (1) 6–24, (2) 25–42, (3) 43–60, (4) 61–78 and (5) > 78. Tree-shrub cover sums are arranged similarly: < 29.6, 29.7–59.2, 59.3–88.8, 88.9–118.4 and > 118.5. The moisture index category 1 represents very dry and category 5 moist. The litter cover sum values are also entered in the stand ordination diagrams (Fig. 16). The classes of some selected soil characters are plotted in relation to the stand ordination diagrams in Fig. 17. The range of each class of these characters are given with the diagrams.

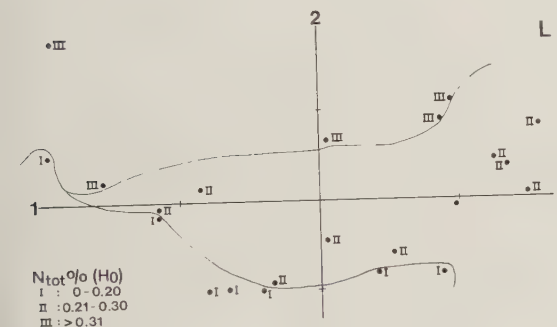
It is apparent from the ordination diagrams in Figs. 15 and 16 that the first axis lies in the direction of the maximum environmental variations from open and very dry meadow stands to mesic and closed deciduous forest stands, or to dry mesic-mesic heath on only one ridge, the Recent ridge. This is emphasized by the very clear relation between the first axis and the microclimatic factors as well as the litter cover sum. The second axis is not related closely or consistently to these factors. However, the second axis separates the stands of the two major vegetation groups of the Recent ridge. On the other hand, the moisture index trend exhibits a curvilinear pattern along the first axis in the diagram of the Litorina ridge stands, starting with the dry stand no. 1, passing the dry mesic-mesic stands of vegetation group (L) and the mesic stands of group (M) up to the moist stand no. 7 in the middle. In the diagram of the

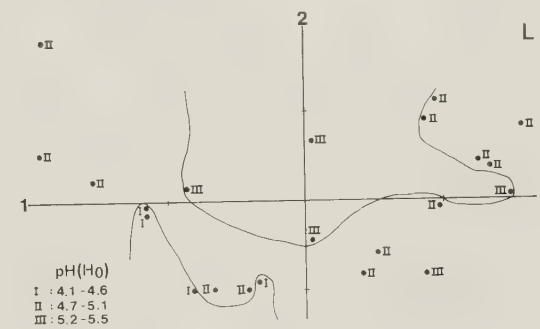


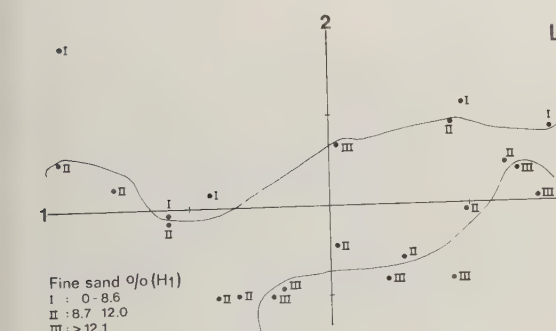












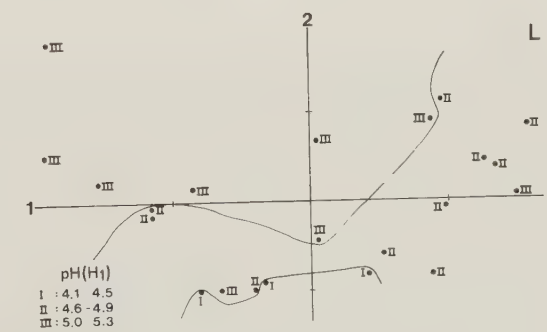


Fig. 17. (continued)

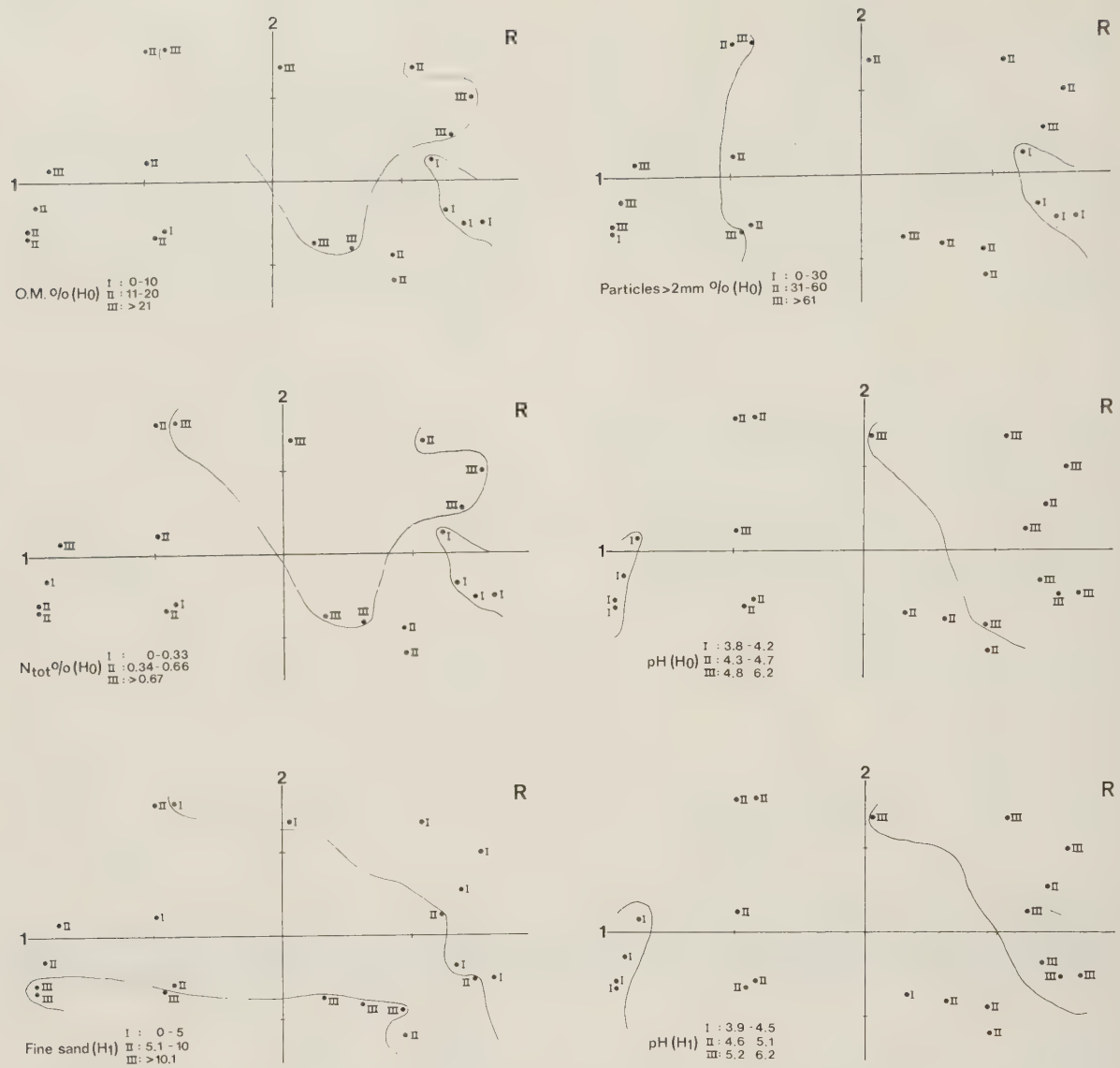


Fig. 17 (continued)

Recent ridge, stand no. 17 has a position in the middle with reference to the first axis, and may be attributed a transitional character among the stands on that ridge. This dry mesic stand, distinguished by a large number of species, is the only one with $CaCO_3$ in its soils, and other soil characters have maximum values there (Table 4c).

The classes of different soil parameters are more or less overlapping in their behaviour in the ordination diagrams. Therefore the approximate patterns of distribution of classes of some selected soil parameters are represented (Fig. 17). The attempt to separate the classes from each other was not successful. However, some aspects of the distribution of some of these selected characters have been put forward. In the stands on the Ancylus ridge, the first axis may be related in H_0 to water holding capacity, organic matter and the fine sand fraction and in H_1 to pH, while the second axis shows some degree of relation to pH in H_0. Similarly, for the Litorina ridge stands, the first axis may be related to particles > 2 mm in both H_0 and H_1; on the other hand, the second axis may be related to water holding capacity, organic matter and N_{tot} of H_0 but to pH and fine sand

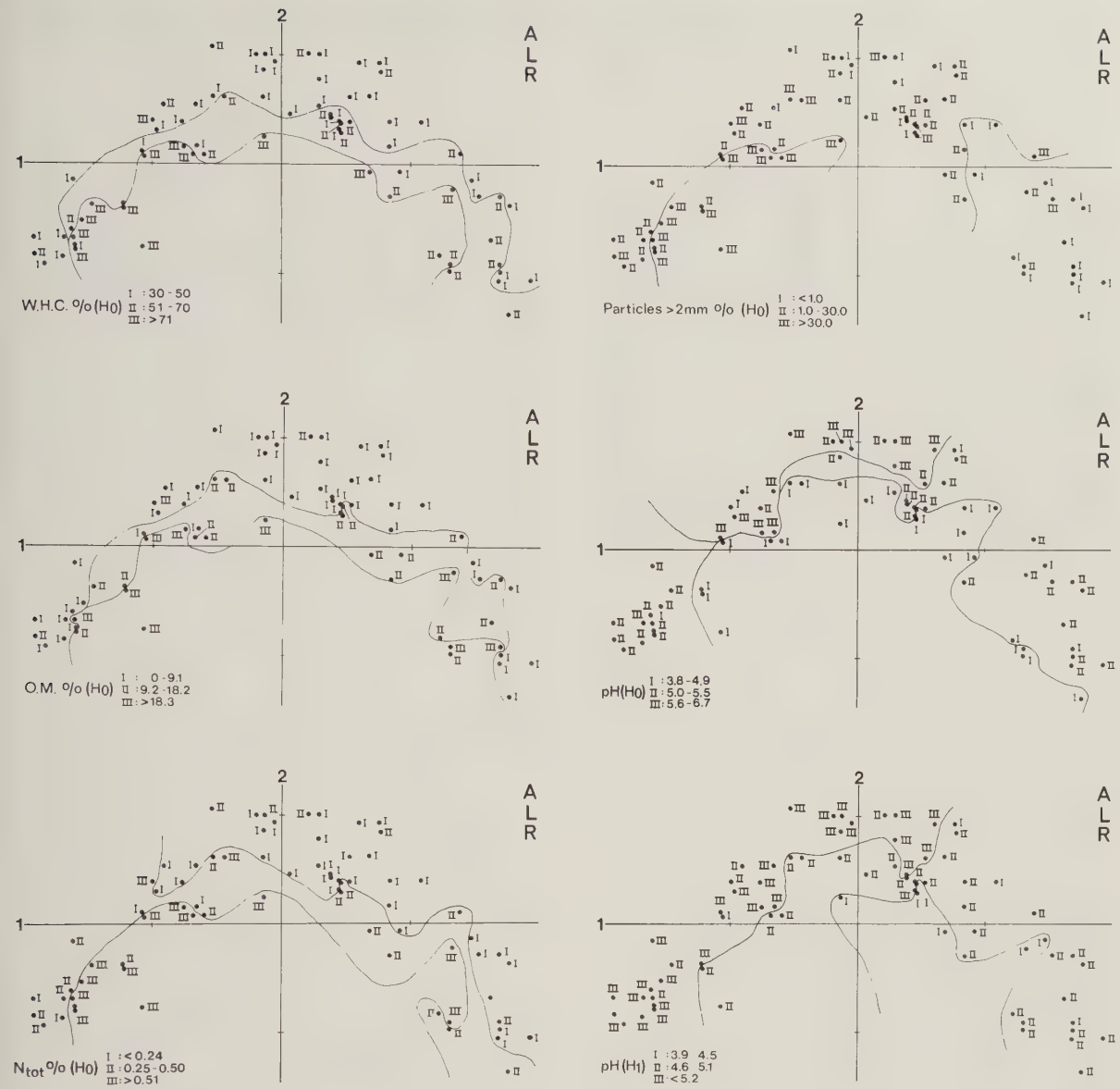


Fig. 17 (continued)

fraction in H_1. In the Recent ridge stands, pH in both horizons and particles > 2 mm in the H_0 may be related to the first axis; but the second axis may be related to fine sand (H_1). Organic matter and N_{tot} in H_0 related to both axes. In the ordination diagram for all the stands together, the first axis is related to particles > 2 mm in H_0; but the second axis may be related to water holding capacity, organic matter, pH and N_{tot} in H_0 and to pH in H_1.

The results of the analysis of soil characters show that they mostly do not show very clear trends of variation relative to phytosociological gradients. Accordingly, it may be concluded that presence, dominance and frequency of species are to a large extent related to the process of stabilization of the vegetation and to microclimatic conditions rather than to differences in soil characters. However, the variations of soil parameters may be too small to have a major ecological effect on the plant cover, since the soil parameters in open and shallow soil with a high content of stone-gravel material (meadow stands), have high values, as well as those in dense deciduous forest stands. Also, the long history of interference by man and animals and the former land-

use in the study area strongly affected the natural balance between the vegetation and soil characters; as a consequence, the relationship between species distribution and soil characters is in several places difficult to define.

The pattern of distribution of species and of environmental variables reveals that microclimatical gradients are correlated to vegetation gradients. The open and dry to very dry vegetation, composed by species such as *Thymus serpyllum, Sedum acre, Galium verum, Artemisia campestris, Saxifraga granulata, Veronica spicata, Festuca ovina* and *Abietinella abietina* is at one end of the vegetational continuum; a more stabilized closed deciduous forest with *Corylus avellana* and *Quercus robur* in the tree-shrub layer, and for example *Hepatica nobilis, Dentaria bulbifera, Mercurialis perennis, Melica uniflora, Maianthemum bifolium* and *Fraxinus excelsior* in the field layer, is at the other end. However, tree-shrub species are included in different successional stages showing increasing stabilization, extending from open and very dry-dry meadow, to dry mesic and transitional with pioneer shrubs such as *Prunus spinosa, Juniperus communis* and *Rosa* spp., and to a later stage of succession with mesic and dense forest of oak and hazel. Rodenborg (1976) placed hazel among the pioneer shrubs. However, the results of the present study indicate that hazel is also an important species in the late stages of succession, as a consequence of the longevity of hazel clones, which have long-lasting underground stems. The vegetation is still dynamic and the "climax" has not yet been reached.

Changes of vegetation in permanent sample plots

The effect of differences in climatic conditions on vegetation properties studied was considerable during the short period of three years. The climate during this period varied significantly, as 1975 was a year with an extremely dry summer, whereas rainfall in July 1977 was abnormally high (Table 1).

Records of permanent sample plots (Tables 11 a–c) indicate that the dry conditions of 1975 had a much more rapid and obvious effect on the field layer in some very dry - dry and open meadow plots than in dry mesic and forest plantation mesic plots. The general decrease of field layer cover in 1975 must be ascribed chiefly to the drought, as many species were killed or wilted and many obviously suffered a check in growth.

Species with some preference for shaded and dry mesic habitats decreased if growing in plots where only survival was possible, being sharply suppressed by drought. For example, there was a decrease in cover of *Veronica chamaedrys* in a dry mesic but open plot from 8 in 1975 to 1 in 1976 and 1977. *Stellaria holostea, Lathyrus montanus, Mnium affine* and *Rhodobryum roseum* disappeared completely in some open and dry plots in 1976.

Graminaceous species e.g. *Festuca ovina, Deschampsia flexuosa* and *Arrhenatherum pratense*, seemed more sensitive to drought than some herbaceous species and also recovered more slowly. This observation is supported by productivity results (see below).

Other herbaceous plants, e.g. *Plantago lanceolata, Helianthemum nummularium, Ranunculus bulbosus, Turritis glabra* and the dwarf-shrub *Calluna vulgaris*, decreased in cover or disappeared in 1976 in some open and dry plots. Other very drought-tolerant semi-woody and herbaceous plants were not affected by the drought, e.g. *Thymus serpyllum, Rumex acetosella, Veronica spicata*, and the mosses *Brachythecium albicans* and *Abietinella abietina*. However, less drought-tolerant species, such as *Rumex acetosa* and *Stellaria holostea* showed a sharp decrease in cover in shaded plots in 1976. The same was true of the annual *Melampyrum pratense*.

Other annual species were evenly distributed in 1976, with high cover degrees in several sample plots, e.g. *Myosotis hispida, Erophila verna, Vicia lathyroides, Trifolium campestre, Trifolium arvense, Cerastium glomeratum* and *Veronica arvensis*. *Taraxacum* also increased. The reason for this was probably the decreased competition from other plants, which still suffered from the previous year's drought.

The number of species recorded in most of the sample plots was higher in 1976 and 1977 than in 1975. It was also observed that the number of species and their cover sum was generally lower in late summer than in the early summer. Several of the typical spring species are obviously not possible to record in August.

The high rainfall in July 1977 may have been favourable to some species, such as *Anthriscus sylvestris* and *Carex hirta*, which had a higher cover degree than in 1975. Seedlings of *Quercus robur* and *Corylus avellana*, and some species of fungi, also appeared as early as August 1977, scattered in some open plots.

The lichens *Cladonia sylvatica, Centraria islandica* and *Cornicularia aculeata* showed a very high stability of cover during the three-year period.

Abnormal climatic conditions not only affected the cover values of several species but also the seasonal development of the vegetation in general. The dry summer of 1975 accelerated development and the wet July of 1977 delayed it, in most of the open and dry plots. It was also observed that the effect of moisture or/and shade may have favoured the flowering of species such as *Agrostis tenuis* and *Arrhenatherum pratense* as compared to open plots.

It was difficult to reveal any trend in the changes of vegetation in the plots in such a short period of time, especially as the vegetation was strongly affected by the varying climatic conditions. The single year of drought may certainly have caused such pronounced dynamic effects that the subsequent reversions might appear as a trend.

Changes of vegetation of open meadows in the study area seem, however, to be related mainly to soil

depth, moisture, and influences of man and grazing animals. The general picture of a successional trend from (a) to (e) may be suggested by the following groups of selected dominant species.

(a) On very shallow, very dry soils: *Cladonia* spp., *C. sylvatica, Cetraria islandica, Polytrichum juniperinum, Pleurozium schreberi.*

(b) On shallow, very dry soils: *Festuca ovina, Galium verum, Campanula rotundifolia, Rumex acetosella, Saxifraga granulata, Polytrichum juniperinum, Abietinella abietina.*

(c) On shallow, dry soils: *Festuca ovina, Galium verum, Arrhenatherum pratense, Helianthemum nummularium, Deschampsia flexuosa, Abietinella abietina, Dicranum scoparium, Rhytidiadelphus squarrosus.*

(d) On deep, dry soils: *Festuca ovina, Poa angustifolia, Phleum phleoides, Arrhenatherum pratense, Agrostis tenuis, Achillea millefolium, Plantago lanceolata, Galium verum, Mnium affine, Rhytidiadelphus squarrosus.*

(e) On deep, dry mesic soils: *Poa angustifolia, Dactylis glomerata, Festuca rubra, Galium verum, Arrhenatherum pubescens, Mnium affine, Cirriphyllum piliferum.*

Standing crop

A factor to be taken into account in the consideration of standing crop is the unusual weather conditions during the first year of the period of investigation of productivity. The changes of climate induced fluctuation in the composition of the plant cover, as mentioned in the previous section.

The extreme drought in 1975 had very marked effects (Table 12). In the open meadow plots the amount of standing crop, and of living material, reached a maximum in May. Although the unusual drought of 1975 had a major effect on the size of the standing crop in the open meadows, there is no such evidence in the productivity values from the low-cover forest plot. Although the fluctuations in climate are considerable, it seems that the maxima of average values of the living material and standing crop there mostly occur in June-July.

In the study area (Table 14) high cover values correspond to high values of productivity.

Tables 13 and 14 show the effects of repeated harvest in the sampling plots. The general trend was that productivity decreased sharply in all the plots as consequence of repeated harvests. This effect was more noticeable for graminaceous plants than for herbaceous ones especially if the plots were harvested both in 1975 and 1976. The graminaceous production in general was sensitive to drought. Recovery after repeated harvests was more rapid for herbaceous plants than for graminaceous ones. The majority of the herbaceous species have relatively deep root-systems and possibly exploited moisture reserves during the dry year whereas several graminaceous species were subject to desiccation. Generally, there is a high peak of amounts of dead material (only field layer litter) during the autumn. One year of rest, with no harvest, was apparently important to the vegetation resulting in a decrease of standing crop of only about 30 % as compared to about 60 % in the continually harvested plots.

It is difficult to make a direct comparison of the three ridges in respect to productivity because there are differences in micro-environmental conditions (Table 14) and in species. Moreover, interference by man has been considerable and not equal on the three ridges. However, graminaceous plants are generally less dominant on the Litorina ridge than on the other two ridges and the soils are more fertile and have remained relatively undisturbed by man and grazing animals during the last three decades. The productivity of the plant cover is therefore higher on the Litorina ridge than on the Ancylus and Recent ridges (see "Discussion").

Discussion

Differentiation of vegetation

Although the Ancylus, Litorina and Recent ridges, in a chronological order, are geologically separate from each other it seems most appropriate to consider the entire vegetation structure of these ridges in the Vickleby parish (Öland), as presented in this treatise, as a continuum. This continuum comprises a large vegetational gradient extending from open meadow to dense deciduous forest. However, the results of classification have made clear the instability and heterogeneity of the vegetation as well as the close relationship between canopy cover and structure of the understory vegetation.

According to a phytosociological study by Sjögren (1964), some deciduous forest stands of the study area belong to the *Betulo-Quercetum melicetosum* and *Deschampsio-Fagetum* associations. This preliminary classification should not discourage attempts at further division of the forest vegetation of the area into subordinate vegetation groups. Furthermore, the non-forest vegetation must also be considered. In the present study, the quantitative data recorded from 73 stands, selected as objectively as possible and including a wide range of variation of the environmental factors, indicate that all the stands are codominated by two or more species. The application of the agglomerative clustering technique was found to be successful in classifying the stands into several characteristic vegetation groups. These vegetation groups are not sharply delimited from each other but are mostly interrelated. Nevertheless, the technique has demonstrated effectively and quantitatively, in a display of the vegetation structure within the study area, the possibility of characterizing a larger number of phytosociological groups than in previous studies.

The following conclusion by Sjögren (1974), in a paper on deciduous forest vegetation on Öland, applies to the situation in the study area, as appraised in the present paper: "There are rarely sharp limits between plant communities in the field. Overlapping species are generally present on both sides of the sociological boundaries between two or several communities. The frequency of presence of a species in one, or in two or several communities indicates the differential value. Descriptions of plant communities often over-emphasize the differential species with the highest differential values. A description of the whole group of species with a differential value is much more useful in tracing habitat conditions."

Relationship to environmental conditions and succession

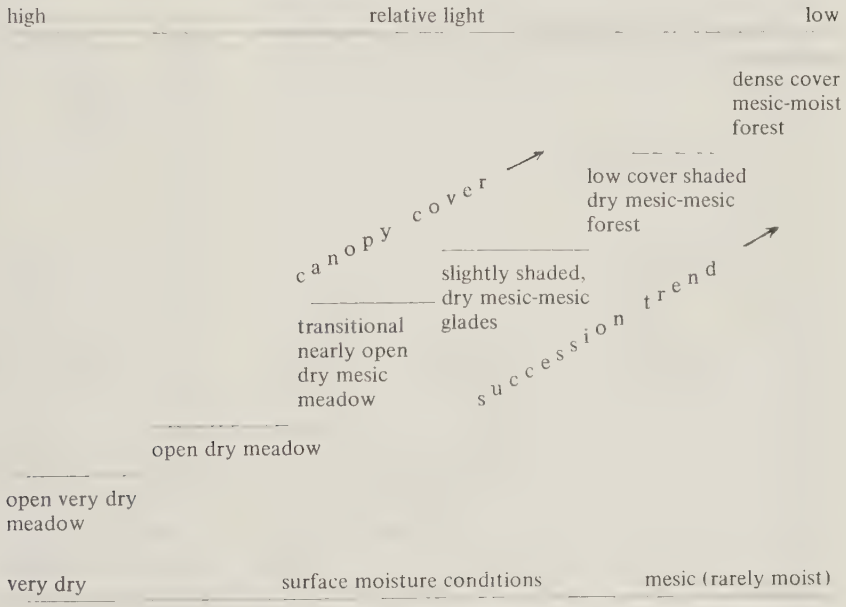
The aim of this study was to elucidate the main relationships between the differentiation of vegetation and available data on environmental conditions. However, the vegetation groups extracted by the agglomerative classification show a clear pattern, also evident in the ordination diagrams. The separation of vegetation groups along the first two ordination axes suggests that groups of interrelated factors control the ecosystems. These factors could be divided into two main groups: those dependent on the vegetation, such as light, moisture regime, canopy and litter cover, and to some extent soil depth and pH; and those not dependent on the vegetation, including the other soil variables examined. Factors in the first group are generally correlated with the degree of stability of the vegetation and with gradual successional changes towards deciduous forest dominated by *Quercus robur* and *Corylus avellana*. The reason why factors of the second group are not correlated with the vegetation, as defined in the delimitation and arrangement of stands, may be various kinds of disturbances, for example influences of man and animals. Their intensity and quality have been different from time to time, but have dominated the long history of development of this vegetation. In large parts of the area this interference has apparently obscured the possible interaction between the vegetation and several of the soil characters. It is probably a consequence of this interference that it is mainly the soil variables of the second horizon (H_1), which are per-

haps most stable, which show significant correlations with the vegetation gradients. The structure of the vegetation is still quite mosaic, but the rate of successional changes has increased after gradual decrease of interference. Wells et al. (1976) also considered the differences in soil chemistry between their majority of grassland-types of different ages and land-use at the Porton Ranges, England, to be the result of the influence of the grassland succession, post-cultivation management, and soil faunal activity, rather than being a primary cause of the observed vegetation differences.

Influences of disturbance on succession were not examined directly in this study but it can be concluded that there is a close correlation. For example, a fenced area somewhat distant from tourists' activities, on the Litorina ridge, has been invaded by dense deciduous forest. On the other hand, large areas in other places are subject to frequent trampling by tourists or by grazing cows (e.g. the vegetation group "K_1" on the Litorina ridge and "G" on the Recent ridge, which are now open and very dry-dry meadows). In short, a disturbance and succession gradient is suggested by the alignment of stands along the first axis of the ordination diagrams; the undisturbed successional trend naturally proceeds in parallel to an increase of tree-shrub cover sum, while disturbances have the opposite effect. The presence in some stands of species which are not normally present in dry meadow vegetation and not typical of it may indicate that the study area has been subjected to a fairly high degree of disturbance, e.g., *Polygonum convolvulus, Lolium perenne, Erigeron acre, Matricaria inodora, Geranium robertianum* and possibly *Chrysanthemum vulgare*. In addition, many accidental species were recorded only once in the stands studied (Table 2).

The presence of typical open meadow species in some fairly dense deciduous forest stands, e.g. *Galium verum, Campanula rotundifolia, Stellaria graminea* and *Hypericum perforatum*, demonstrates that the vegetation studied is still unstable. The highly frequent species in this study are mostly such less exclusive open meadow species as *Galium verum, Poa angustifolia, Campanula rotundifolia, Agrostis tenuis, Veronica chamaedrys* and *Achillea millefolium* (cf. Table 2). It is likely that the deciduous forest stands now present on the ridges were more open before 1937, when a large area of Vickleby parish was purchased by the Swedish Sugar Company (see Ekstam & Sjögren 1973).

The main trend of succession in the study area is towards deciduous forest, independently of the starting point. The general picture of this trend may be deduced from the vegetational gradients in the following diagram:



Moisture. Of the several environmental factors considered in this study, moisture regime and light appear to be of overriding importance in controlling the vegetation structure but are also affected by it, because of its control of insolation. On the other hand, there were no very clear relationships between the vegetation structure and environmental factors thought to be associated with available soil water (hygroscopic moisture and water holding capacity). Similarly, Swan & Dix (1966) in their study of the Upland forest at Candle Lake (Canada) found no obvious relationships between vegetation pattern and moisture regime as expressed by drainage regime, hygroscopic moisture and water retaining capacity. It then seems likely that the moisture parameters involved are related to insolation, heating the soil surface. Possibly the depth of soil and the position relative to a temporary subsoil water table in very wet periods may also have an effect (the latter only for the moist stand). Pettersson (1965) attributed fluctuations in the water economy of the island of Öland to the presence in large areas of only thin Quaternary deposits as well as to the unusually large fluctuation in climate.

It is therefore difficult to find a single environmental factor that can fully express the moisture regime in this study. Nevertheless, the vegetation moisture index (Rowe 1956; Waring & Major 1964; see further the section on methods), which is based on elevation of the stands and mean field-layer species cover, has shown a clear-cut relationship with the vegetation gradient. However, mean field-layer cover may be affected by several factors other than moisture, e.g. very dense shade, available nitrogen, and climatic growth factors, and also by the phenology of the species. Thus the vegetation moisture index cannot be generally applied but is of only local applicability.

It is claimed that the vegetation moisture index may sometimes provide more information than soil measurements about stand conditions. It is appropriate to mention the words of Albert Einstein (1940) quoted in Loucks (1962), about factor synthesis: "The sense-experiences are the given subject matter. But the theory that shall interpret them is man-made. It is the result of an extremely laborious process of adaptation: Hypothetical, never completely final, always subject to question and doubt."

Irradiation. Vegetation composition could not be correlated to degree of slope or to aspect because the ranges of variations of these factors are not sufficiently wide to make any effective difference in the amount of radiation reaching different stands. However, stand elevation plays an important role in determining vegetation composition and stands condition. The microtopographic trend may be parallel to the moisture trend, in this study.

Light and canopy cover, which are of course strongly negatively related, control the understory species. Variation in pH is fairly small and is attributable mainly to differences in kinds of litter. There is a relatively smaller number of understory species in closed deciduous forest stands with *Corylus* and/or *Quercus*, where pH is relatively high, than in open meadow stands; also there is a relatively larger number of understory species in some transitional stands than in low-cover forest stands, although moisture and pH are fairly similar, suggesting that light (or total irradiation) is the primary controlling factor (Oosting & Kramer 1946; Swan & Dix 1966). The bottom layer is even more sensitive to light changes, and it was found that some species do not tolerate the conditions in dense deciduous forest stands. Because of shade, and possibly because of too much litter, these species are absent or almost so from such habitats.

The mean total number of species per stand category of the field and bottom layers gradually increases with increasing relative light as follows:

relative light percent range	mean total number of species field layer	bottom layer	number of stands
6–24	30	2	14
25–42	36	3	12
43–60	37	4	10
61–78	35	5	8
79–100	41	6	29

It should also be mentioned that some fairly typical forest species, for example *Maianthemum bifolium, Mercurialis perennis, Melampyrum pratense* and *Stellaria holostea*, can grow occasionally in open meadow where they may sometimes be more or less shaded out by other species (Køie 1951; Ekstam & Sjögren 1973).

Light distribution is very uneven within the stands. This was expected, since light, more than any other factor, is influenced by the canopy which in turn is

subjected to human interference of various kinds. The difference in light supply in a small area may therefore be responsible for the mosaic structure of the understory vegetation. Hence, the presence of some typical open meadow species under tree canopies was also expected. *Quercus robur* trees with *Corylus avellana* in the tall shrub layer give more shade than *Q.r.* alone or than *Betula verrucosa*. Measurements of relative light thus showed large differences in dependence both on tree-shrub cover sum and tree-shrub species combinations (Tables 9a–c).

Some species, such as *Oxalis acetosella,* are highly shade-tolerant species, present in both *Betula* and *Pinus* plantations and in *Quercus* and *Corylus* woods. On the other hand, species such as *Maianthemum bifolium, Mercurialis perennis* and *Dentaria bulbifera* are shade-tolerant species here mainly growing in *Quercus* and *Corylus* woods. Within the forest stands, some species have their maximum occurrence at certain positions along the shade gradient. For example, *Stellaria holostea* grows preferentially at forest edges, with *Convallaria majalis* close to the edges but inside the forest, and *Maianthemum bifolium* in the forest interior. However, the same species may behave differently in different types of deciduous woods and in *Pinus* plantation stands. Both the deciduous woods and the *Pinus* plantations may provide appreciable variations in exposure, leading to a similar appreciable variation in local climatic conditions (Sjögren 1974). The age, size, and growth type of trees and shrubs should also be taken into account.

In very dry open meadow stands, such as on the Recent ridge, the full exposure to light naturally means a superficial desiccation of the soils. In such open habitats, air temperatures were higher and relative humidity values were lower, than in deciduous forest habitats. Soil temperatures are also likely to be higher, at least on sunny days. Therefore, vegetation in such stands may differ as a result of differences in total insolation, not only light, i.e. differences in the effect of energy supply (Køie 1938).

It is difficult to establish any relationships between light (or total insolation) and physical soil characters, although it is possible to show correlations with some chemical soil characters. Since different canopies of tree and shrub species produce different kinds and amounts of litter, leading to variations in pH and available nutrition, it is likely that such correlations are not directly due to insolation, but to cover of woody species which affects both energy and soil properties.

In conclusion, the relation between differentiation of the vegetation of the study area and insolation is very important. For an extended understanding of light as an important ecological factor, see also papers by: Køie 1938 and 1951; Sjögren 1961; Waring & Major 1964; Bainbridge et al. 1966; Wali & Krajina 1973; Bråkenhielm 1977.

Acidity. pH is relatively high in most of the transitional stands, which may explain the comparatively large number of species in such stands. However, in some stands, situated in between other stands dominated by *Calluna vulgaris* or *Juniperus communis* or in *Pinus* plantations, low pH values and relatively low numbers of species have been recorded. The plants themselves play a significant part in determining the species structure of a stand (Swan & Dix 1966; Kershaw 1973; Bråkenhielm 1977). Thus, pH values in most of the stands studied are slightly lower than those measured in former pasture on central Öland (Rodenborg 1976). In both cases, some decrease in pH may be attributed to the effect of air-dry storage of the soil samples; Sjörs (1961), Bråkenhielm (1977) and others indicated that pH values usually decrease during the dry storage. The comparatively low pH of some sites may be due to the fact that the soils contain no $CaCO_3$, which may have leached down to depths below 40 cm, as observed by Ingmar & Moreborg (1976) in till in a rich calcareous area in northern Upland, Sweden. However, the pH is also influenced by the litter supply from the vegetation itself.

Soil indicators. Species which show considerable quantitative changes along environmental gradients with small gradual variations may be regarded as good indicators of the environment. Examples of these are *Thymus serpyllum, Veronica spicata, Artemisia campestris, Saxifraga granulata, Sedum acre* and the bryophyte *Abietinella abietina*, which show a considerable local preference for sites of more or less shallow, poor and coarse-textured soils in very dry open meadow (though some, e.g. *Artemisia campestris*, can develop deep root systems on deep soils). Another group of examples include *Dentaria bulbifera, Mercurialis perennis, Melica uniflora* and *Hepatica nobilis*, which are indicators of more or less deep, rich and often fine-textured soils in fairly dense mesic deciduous forest.

Principal components analysis

As has been discussed in many other studies, the principal components analysis (PCA) is a useful tool for simplifying a multivariate vegetation structure in order to identify the major environmental variation trends within it. Van der Maarel (1969) suggests that drawing the "isocenes" in a PCA ordination diagram may be useful for clarification of the visual trends of variation along the phytosociological gradient axes.

Some authors have criticized the use of PCA as an ordination technique because it produces some degree of curvilinear (bell-chaped) distortion, implying that the axes abstracted may consequently become uninterpretable or ecologically meaningless. Increasing range of community variation (beta-diversity) leads to curvilinear distortion in PCA (Noy-Meir & Austin 1970; Swan 1970; Jeglum et al. 1971; Austin & Noy-Meir 1971; Gauch & Whittaker 1972; Beals 1973; Whittaker & Gauch 1973; Dale 1975; Kessel & Whittaker 1976; Gauch et al. 1977), but it is impossible to limit beta-diversity in studying the major variation in the composition of vegetation and environment in an area (Bouxin 1976). Austin & Noy-Meir (1971) stated that all the present ordination techniques are subject to curvilinear distortion except the original study by Curtis & McIntosh (1951).

The curvilinear distortion leads to loss of efficiency of PCA, but this is not sufficient reason to reject the method (Feoli-Chiapella & Feoli 1977). Some efforts have therefore been made to find a transformation or standardization in order to linearize the stand or species correlations in a study area (cf. for example Swan 1970; Beals 1973; Gauch 1973; Gauch et al. 1974; Noy-Meir 1975; Noy-Meir & Whittaker 1977). However, Goldsmith (1973) said that: "From the ecological viewpoint, the ordination from data standardized by species appears to have no advantage over the ordination from raw data. Standardization of the raw data by stands produces only a uniform scatter of points with a similar arrangement to that using unstandardized data." Data transformation does not then seem to give results significantly different from those obtained with untransformed data (Dagnelie 1960 and Orlóci 1966).

Goldsmith (1973), Howard-Williams & Walker (1974) and Bouxin (1976) found that PCA produced satisfactory results on the basis of high stand diversity and could demonstrate major variations of vegetation structure. The stand ordinations in this study are curvilinear but the results suggest that the range of stand diversity does not exceed the acceptable limits for centred PCA.

Effect of grazing

The effect of grazing on the vegetation of the study area was not directly considered here, since grazing ceased almost completely after 1940 in most of the area, but it is appropriate to compare stands which have been grazed by cows up to 1975 with neighbouring ungrazed stands. The grazed stands of one vegetation group (G_3) and the ungrazed stands of another (G_2), both in open and very dry meadow on the Recent ridge (Table 9c), were used for this comparison. The effect of grazing in the vegetational group G_3 is mainly from manuring and frequent trampling. pH-values were lower in the grazed group G_3, except in stand no. 17 where calcium carbonate was present in the soil, than in the ungrazed group G_2. Similarly, organic matter and nitrogen percentages are considerably higher in G_3 than in G_2.

Vegetation composition of the groups is also different. For example, the following species show lower frequencies or presence in the grazed than in the ungrazed group: *Festuca ovina, Phleum phleoides, Arrhenatherum pratense, A. pubescens, Galium verum, Sedum acre, Allium vineale, Achillea millefolium, Thymus serpyllum, Potentilla tabernaemontani, Plantago lanceolata, Silene nutans, Anemone pratensis, Campanula rotundifolia, Carex arenaria*, and in the bottom layer *Abietinella abietina, Dicranum scoparium, Rhytidiadelphus squarrosus* and *Cladonia* sp. However, some of these species are known to resist grazing fairly well elsewhere, e.g. *Achillea millefolium, Plantago lanceolata* (and probably *Galium verum*).

In contrast, *Cerastium brachypetalum, Aira praecox, Festuca rubra, Galium boreale, Saxifraga granulata, Bromus hordeaceus, Luzula campestris, Anthoxanthum odoratum, Plantago maritima, Lotus corniculatus*, and the bryophytes *Polytrichum juniperinum* and *Hypnum cupressiforme* are more frequent in the grazed group than in the ungrazed one, which, for a few of them, is somewhat surprising. *Galium boreale, Lotus*, etc., are often seen in ungrazed habitats. *Rumex acetosella, Veronica spicata, Ranunculus bulbosus, Veronica arvensis* and the bryophyte *Brachythecium albicans* are examples of species with more or less similar frequencies or presence in both groups.

These results may agree to a large extent with those of Steen (1956), who studied effects of grazing in two areas subject to varying degrees of grazing pressure in a dry meadow at Borgholm (Öland). However, there are some differences; for example, *Veronica arvensis* and *Brachythecium albicans* were considered by Steen as typical of the most grazed phase, while *Veronica spicata* and *Carex caryophyllea* were less abundant in the most grazed than in the moderately grazed phase. *Galium verum, Ranunculus bulbosus, Sedum acre, Plantago lanceolata* and other species were similarly abundant in the two phases, or indifferent towards the grazing phase. But Steen added, referring to his previous work (1954), that *Galium verum, Plantago lanceolata* and *Carex caryophyllea* can be included as typical of heavily grazed areas. This difference may be attributed to the kind of grazing animals in the area described by Steen, namely sheep and horses. Differences may also be due to differences in soil factors, and to the limited area of the stands compared, which allows random heterogeneity and chance alone to play a part.

The soils in the grazed vegetation group of stands (G_3), were easily eroded by animal grazing and trampling. The grazing effect created a "disclimax", characterized by a considerable increase in the number of annual species with low competitive ability, such as *Bromus hordeaceus, Erophila verna*, and *Aira praecox*. Dominant perennials, for example *Festuca ovina, Galium verum, Carex arenaria* and *Pimpinella saxifraga*, in the ungrazed group (G_2) are favoured by coarse texture, depth and stability of the soil and may increase during the successional sequence after cessation of grazing.

In central California, Elliott & Wehausen (1974) found that the removal of cattle caused a successional change towards a "climax". Heavy grazing was responsible for considerable reduction of the number of native species if compared with conditions in plots left ungrazed for six years. However, grazing also caused a considerable decrease in the number of the perennial and biennial species. Introduced perennials such as *Rumex acetosella, Lolium perenne, Plantago lanceolata* and *Hypochoeris radicata* were retained as part of the "climax" community.

Rosén & Sjögren (1973) have outlined five successional stages of the vegetation caused by sheep grazing on the southern limestone heath (Alvar) of Öland, and they found that ungrazed *Avenetum* became invaded by shrubs such as *Juniperus communis*. They also showed considerable differences between grazed and ungrazed *Avenetum* in respect of the herbaceous plants and suggested that many of the herbaceous plants tolerate grazing. However, they concluded that the relationship between the grazing and the vegetation structure is very complex.

Production

The annual production can be estimated by three different methods: (1) the increment method, by summing the positive differences in the standing crop between repeated harvests while assuming that the standing crop at the beginning of the growing season is zero, (2) the maximum standing crop method (Persson 1975), or (3) by difference between maximum and minimum standing crop (Ovington et al. 1963). The way in which the above-ground standing crop of the field-layer species is determined varies with the method (cf. for example Rawes & Welch 1969; Wallentinus 1973; Baradziej 1974; Persson 1975). The three methods involve very easy calculations but give considerably different results. It is apparent that method (1) gives equal or higher results than method (3). All methods would give higher results when calculated for each individual species separately than when calculated for groups of species, as in the present investigation.

The mean primary production over the years 1975—1977 of the four harvest plots was estimated by the increment method (1) as 336.5, 339.2, 445.9 g/m^2 for the first three open and dry meadow plots, on the Ancylus, Recent and Litorina ridges, respectively, and as 185.1 g/m^2 for the low-cover, and dry mesic forest plot on the Litorina ridge; while by the maximum above-ground method (2) the production was calculated for the same four plots as 256.0, 291.2, 420.3 and 183.5 g/m^2, respectively; but according to the third method the production for the same plots was only 189.3, 230.4, 332.3 and 123.7 g/m^2, respectively. The third method is not suitable for accurate assessment of production (Baradziej 1974).

Whereas the general state of the productivity showed considerable seasonal differences and some fluctuation from year to year (Fig. 18), all the species of the sampling plots did not reach their stage of maximum development in the same month, but their individual maxima occur at various times during the

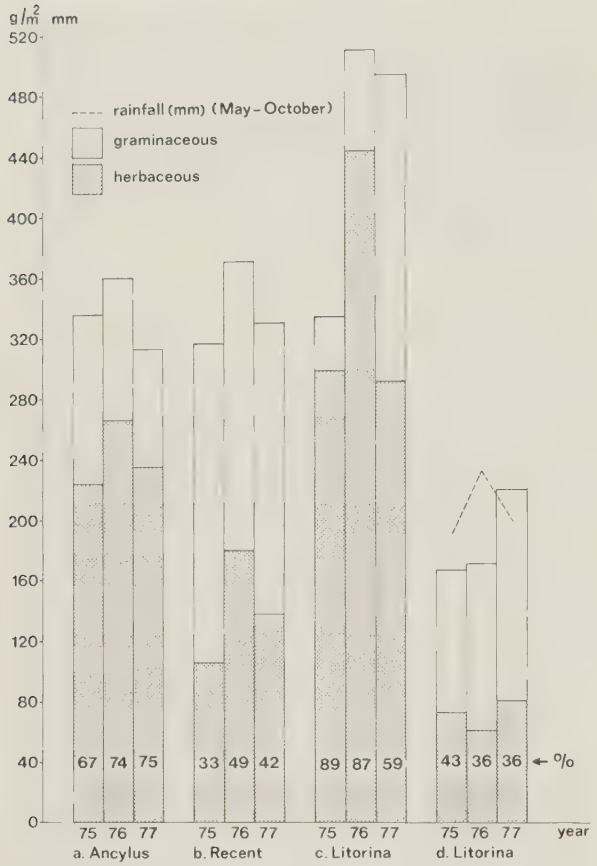


Fig. 18. Living standing crop of four harvest plots (a, b, c = open and dry meadow on the Ancylus, Litorina, and Recent ridge respectively, and d = low cover dry-mesic deciduous forest on the Litorina ridge) in 1975–77. Stippled areas represent living herbaceous material; white areas represent living graminaceous material. Percentages are given for herbaceous plants. The broken line shows the total rainfall (mm) during the summer months (May–October) in 1975–77.

greater part of the growing season. The maximum standing crop cannot therefore be taken as a measure of the total productivity, when based on groups of plants. Although the increment method gives much higher values than the maximum method in only the open meadow plots, and fairly similar results in the low-cover forest plot on the Litorina ridge, it is the only acceptable method for the vegetation of the study area.

As Persson (1978) pointed out, in the increment method, statistically uncertain small positive increments are treated as a real increase, so the method could give results which are too high. On the other hand, when groups of species are considered instead of individual species, a decreasing effect is introduced which may or may not counterbalance the possible positive error due to random variation. Also much of the real increments will be missed because of insufficiently frequent sampling. Finally, some growth takes place even in periods of overall decrease, and this will also be missed. Persson (1975) found that even the total increments for above-ground plant groups gave too low a measure. The increment method has been widely used and recommended in grassland studies (Milner & Hughes 1968).

Comparison with other data. There has been no previous investigation of the productivity of shore ridge vegetation on Öland so comparative data are available only for the productivity of grassland and low-cover deciduous forest habitats in other places in Sweden or elsewhere. In the literature, the annual production of moist or wet meadows is generally higher than in dry meadows, and it is usually also higher in open habitats than in the field layer in shaded or closed forest stands. While investigating sheep pastures on the limestone heath (Alvar) on Öland, Rosén & Sjögren (1973) estimated the standing crop in 1969 (a dry year) in ungrazed *Avenetum* as 295 g/m^2 and in ungrazed *Festucetum* as 133 g/m^2.

In central Sweden, Dalarna province, the production of three different meadow types called *Flexuosetum, Hypochoeridetum* and *Eu-Geranietum*, was estimated by Sjörs (1954) as 110–120, 87–137 and 147–195 air-dry g/m^2, respectively. This was based on a single harvest of hay and was not intended to provide figures for the whole standing crop. Persson (1975) concluded that these figures should be increased by some 30–40 % to be comparable with results of the total harvest method at a later time of cropping (cf. Persson 1975). Nilsson (1968) gives figures of up to 500 g/m^2, with averages of about 300 g/m^2, for production in hay meadows in southern Småland (S Sweden), while Tinnberg & Alm (1969), as quoted by Wallentinus (1973), give a figure of about 490 g/m^2 for the terrestrial ridge meadows at the Tullgarnsnäset (Sweden).

Marshy, wet or moist habitats are generally highly productive. For example, Steen (1957) estimated the productivity of an ungrazed marshy shore meadow at Lake Mälaren (central Sweden) at 426 g/m^2. In Baltic coastal meadows, in an area 125 km SSW of Stockholm, Tyler (1971) recorded 161 g/m^2 as

maximum above-ground biomass, while Wallentinus (1973) employed different methods of productivity calculations and arrived at a figure of 324–430 g/m^2 for a Baltic coastal meadow area 45 km SW of Stockholm.

Andersson (1970b) estimated the productivity of a wet meadow in the south of Sweden as 720 g/m^2. In three ecosystems of *Filipendula ulmaria, Carex flacca* and *C. caespitosa*, he obtained figures of 470, 331, 417 g/m^2 production, respectively, while the field-layer productivity in a forest stand of *Quercus robur, Tilia cordata* and *Corylus avellana* was 77 g/m^2, and he suggested that the turnover was more rapid in the meadows than in the woodland. Persson (1975) in his study at Andersby, E central Sweden, pointed out the negative correlation between field layer development and canopy density. Clearing the woodland brought about an increase in the growth of the ground flora. He gives figures for field-layer production of 130–160 g/m^2 in slightly shaded *Betula* pasture land with *Calamagrostis arundinacea*, 100–130 g/m^2 in thinned mixed woods and 50–80 g/m^2 in unthinned woodland with half-open former glades. Similarly, in former hay meadows, now neither mown nor grazed, in Garpenberg in SE Dalarna (Sweden), Samuelsson (1966) observed a decrease in field-layer production as forest and shrub canopy development increased. Along a transect, he found that field-layer production decreased from 175 g/m^2 in *Calamagrostis arundinacea* glades to only 18 g/m^2 under a closed canopy of *Corylus avellana*.

Ovington (1955) also stated, in his study of the development of woodland in England, that the total weights and percentages of dry matter of the herbage in open plots were much greater than in corresponding forest plots and concluded that the ground vegetation gives an indication of stand conditions.

In Poland, Aulak (1970) estimated the production of the field layer of the *Circaeo-Alnetum* association as 107.5 g/m^2, while Baradziej (1974) estimated the productivity of a *Carex gracilis* community as 500–550 g/m^2 and of an *Iris pseudacorus* community as 700–800 g/m^2.

Gorham (1974) gave the air-dry weight of the standing crop in almost pure stands of several *Carex* species in eight different localities covering a wide range of climatic, physiographic and geographical variation. He concluded that the range of above-ground biomass of these communities is between 170 g/m^2 and 1470 g/m^2, and he found a strong correlation between the summer temperature and the standing crop of these sedge meadows in northern and middle latitudes. Among his localities, he included two wetland localities in Sweden, the first in Scania (S Sweden), with 600 g/m^2 (Mörnsjö 1969) and the second at Abisko (N Sweden) with 270 g/m^2 (Pearsall & Newbould 1957).

Al-Mufti et al. (1977) estimated the sum of maximum standing crop and litter in three grassland stands (with many species in common with the open meadow plots of this study) in Lathkilldale and North Anston in England as ranging from 400 to 800 g/m^2. They concluded that their study results were related to species-density in herbaceous vegetation.

These records in the literature show that the measured productivity of the three ridge plots in the present study was fairly high for such dry sites, and this may be expected in limestone grasslands on Öland. However, the productivity is low in comparison to mesic and moist ecosystems.

Variation in time and local space. The general state of the standing crop shows considerable fluctuation from year to year in the three ridge plots, corresponding to the changes in climate during the three-year study period (Fig. 18). The results presented in this figure suggest strong correlations between the size of standing crop in the open vegetation and the amount of rainfall. The standing crop is of course also related to the composition and structure of the vegetation at each site.

The fluctuations in the size of standing crop are more moderate in the open and dry meadow plot on the Litorina ridge, which is dominated by *Geranium sanguineum* and *Helianthemum nummularium* (> 80 % cover value, Table 14). van Gils & Kovács (1977) mentioned that *Geranium sanguineum* communities developed well on limestone soils that had been subjected to mechanical disturbance and used for haymaking, and colonized rapidly in open mesophytic or/and mesothermic sites. In the present investigation *Geranium* in Öland attained its maximum development in late June and was very sensitive to the amount of rainfall, although it is mainly a species of fairly dry and sunny sites. It was greatly suppressed by the drought in 1975, but the year 1976 was very favourable since the rainfall from April–June was quite adequate for its growth. In 1977 the amount of rainfall fluctuated strongly during the summer months. For example, the rainfall in May was the

lowest for more than 10 years, but July had extremely high rainfall. It seems that the amount of precipitation during May and June 1977 was insufficient for full growth of *Geranium sanguineum*. Thus in 1977 this species showed a low competitive ability against the grasses, which were highly represented (cf. van Gils & Kovács 1977). On the other hand, fluctuation of the climatic conditions were not as pronounced in the forest plot, since the trees and shrubs form an effective barrier and the climate under the canopy is considerably different from that above (Ovington 1955). The composition and physiognomy of the field-layer in woodlands is therefore more sensitive to the stand conditions which affect the soil properties, such as shade and litter fall, than to climatic conditions (except under very long-lasting droughts).

Nevertheless, the data about the standing crop do not reveal very much about differences between the ridges, because the samples taken were not adequate to show the wide variations between the different habitats on each ridge. However, the production of the herbaceous group of species varies considerably between the three open meadow plots on the ridges. The herbaceous production in these plots gradually decreased (Fig. 18), in order from the Litorina to the Ancylus and to the Recent ridge. Since most of the herbaceous species are more competitive than the graminaceous ones, and were usually prevalent on the more mesic and fertile soils, it seems that this local variation coincided with the variation between the ridges. This trend coincides with the relationship of productivity with succession in the open meadows (Odum 1960), since the productivity was closely related to vegetation structure and vegetation structure is in a dynamic state. It could therefore be concluded that the Recent ridge offered less possibility of vegetation development than the other ridges, while the Litorina plot was the most productive. It is not surprising that the "climax" of vegetation—if any—in the study area was approached on the Litorina ridge rather than on the Ancylus ridge.

Recommendation for grazing. The investigation into the productivity of the ridge vegetation yields some data on which to base future action in the field of nature conservation. First, the seminatural vegetation on the shore ridges, especially on the Litorina and Ancylus ridges, may provide a better alternative for animal grazing than the vegetation of the flat "Alvar", with its thin soil-covering which is threatened by severe damage as a result of overgrazing by sheep (Rosén & Sjögren 1973). Secondly, the present study suggests some recommendations for a better balance between grazing requirements and the vegetation. These parallel the results obtained by Rosén & Sjögren (1973) for the "Alvar" vegetation. If it is assumed that the harvest method which was used simulates the grazing process, grazing should be regulated. If possible, the period of grazing should not be extended indefinitely in the same area. At least every second year there should be a rest period; while grazing should also be stopped (in areas dominated by graminaceous plants) or limited (in other areas) during extreme drought years. The rest from grazing is very important in preventing from overgrazing symptoms as far as possible.

Phenology

An accurate assessment of the species phenology could not be made from the results of following the seasonal variation in the permanent plots. The phenology was not followed through the whole growing season. Like productivity, seasonal variations are controlled by the climate. Despite the differences in local microclimate and microenvironment on the three ridges there is not much variation in phenology of the same species along the ridges. However, it is possible that drought is more pronounced on the Recent ridge than on the other two ridges, causing graminaceous and herbaceous plants to cease growth earlier. This suggestion is supported by the larger amount of standing dead material in summer on the Recent ridge.

Summary

The treatise concerns the vegetation on three shore ridges, the Ancylus, Litorina and Recent ridges, which locally dominate the coastal landscape of the south part of the limestone island of Öland in the Baltic. The study area is situated along the western coast of the island, in the parish of Vickleby, where the ridges are distinctly separate from each other and are thus suited to a comparative study.

The vegetation studied has been influenced by man and animal for centuries, although now to only a small extent. The present picture of the mosaic vegetation therefore involves strongly dynamic trends. To determine the structure of this vegetation, 73 stands, situated at a maximum distance apart of 2 km along the ridges, were selected objectively in order to incorporate the widest possible range of floristic and environmental variations. The major environmental factors considered were light, moisture, canopy cover, elevation and effect of animal grazing. The vegetation moisture index proved useful in describing the moisture condition of the stands. This index incorporates the mean cover of the field-layer species and the position of the stands in terms of the microrelief.

Temperature, relative humidity and wind velocity were recorded in five selected habitats to provide local climatic data. The local climate was found to differ between the ridges and between the different vegetation types. The local climate as well as the general climate of Öland showed considerable fluctuations, even over short periods of time.

The edaphic characters considered were: the soil depth, soil water (hygroscopic moisture and water holding capacity), organic matter content, pH, total nitrogen, calcium carbonate content, conductivity, titratable acidity, cation exchange capacity, total exchangeable bases for the cations Na^+, K^+, Mg^{2+}, and Ca^{2+} and soil texture. It was found that most of these characters varied significantly horizontally and vertically along the stands.

Texture analyses showed that the soils in all stands are sandy with average percentages ranging from 88.7—93.1 % of the gravel-free fine soil in the surface horizon (H_0) and from 92.9—95.6 % in the horizon below (H_1). The medium sand fraction was the highest (> 50 %) of the sand fractions. The fraction of particles > 2 mm (gravel + stones) varied widely, with 2.5 % (Ancylus), 12.5 % (Litorina) and 67.7 % (Recent). The range of mean pH values was 4.7—5.4, with gradually lower values from the Ancylus towards the Recent ridge. The soils were more acidic in the surface horizon than in the horizon below. Soils were $CaCO_3$-free, or almost so, down to 40 cm. Ca^{2+} had the highest values of the cations, in H_1 1.3 meq./100 g (Ancylus) to 4.2 meq./100 g (Litorina), in H_0 from 4.6 meq./100 g (Ancylus) to 7.1 meq./100 g (Recent). Soil depth differed markedly between the three ridges, gradually decreasing from the Ancylus towards the Recent ridge. Other soil characters also showed wide ranges of variations.

In general, there were large differences in soil depth and drainage between the shore ridges.

The distribution of field layer species along the gradients of microclimate indicates that the habitat of the study area is not one homogeneous unit. Some species were regarded as indicators of particular habitats. None of the species was a leading dominant of all the stands. In the tree-shrub layer, *Quercus robur, Corylus avellana, Betula verrucosa* and *Juniperus communis* were local dominants on the three ridges. In the field layer, six open meadow species were highly frequent, namely, *Galium verum, Campanula rotundifolia, Poa angustifolia, Agrostis tenuis, Veronica chamaedrys* and *Achillea millefolium*. In the bottom layer, only *Mnium affine* was highly frequent.

The frequencies of the field layer species were used to construct the ordination and classification programs. Only species which attained > 5 % presence on one ridge or on all ridges together were considered. The results of the phytosociological analysis showed that the vegetation in the study area is unstable and heterogeneous, but could be differentiated into vegetation groups. The agglomerative

classification indicated a close relationship between canopy cover and the structure of the understory vegetation.

Principal components analysis (PCA) was a useful tool to simplify the multivariate vegetation structure and to abstract the major trends in environmental variation. PCA produced satisfactory results for this highly variable vegetation and the heterogeneity in the stands did not impede or reduce the effectiveness of PCA.

The analyses of ordination and classification were complementary and provided insight into the nature of the factors controlling the vegetation. They helped to characterize many phytosociological groups which had not been described before. These vegetation groups are not very distinct and are mostly interconnected. They are distributed along a successional gradient of increasing stability extending from open and very dry to dry meadows with for example, *Thymus serpyllum, Sedum acre, Artemisia campestris, Festuca ovina, Galium verum* and *Abietinella abietina*, through dry mesic and transitional sites, with pioneer shrubs such as *Prunus spinosa, Juniperus communis*, and *Rosa* spp., to more stabilized mesic closed deciduous forest, with *Quercus robur* and *Corylus avellana*.

Although the three ridges are of different age, the vegetation structure of these ridges as a whole, as well as that on each one individually, was to be considered as a continuum. The pattern of distribution of species and environmental variables revealed that microclimatic gradients, governed by canopy cover, light and moisture, controlled the vegetation gradients. The microclimatic factors therefore appeared to be of overriding importance in this study.

There are two groups of interrelated factors that control the vegetation of the study area, viz. the vegetationally dependent factors, including the microclimatic factors, litter cover, and to some extent soil depth and pH; and the vegetationally independent factors, including the other soil characters. The first category is generally related to the degree of instability of the vegetation, i.e. the successional sequence. The second category refers to disturbance. The influence of man and animal, resulting from changes in land use, have dominated the long history of development of the vegetation. Such influence is nowadays reduced to various tourist activities and short periods of grazing. These influences have very much masked the mutual interaction between vegetation and soil conditions; no highly significant correlation between the vegetation and soil characters was found, and no distinct relationship between the compositional gradients and soil characters could be seen.

The role of light as an important factor was discussed. The main trend of succession in the study area was outlined. The effects of grazing in two neighbouring sites were studied and it was found that cessation of grazing led to successional changes.

The annual above-ground production was measured by three methods. The increment method seemed to give a true but minimal measure of production. The above-ground production for the years 1975—1977 was estimated by this method to be 336.5, 339.2, 445.9 g/m^2 for three open dry meadow plots on the Ancylus, Recent and Litorina ridges, respectively, and 185.1 g/m^2 for the field layer of a low-cover *Quercus robur* forest plot on the Litorina ridge. Standing crop and annual production differed considerably from year to year on the three ridges. Production in the open meadows appeared to be strongly correlated with the amount of rainfall. These results may be used to suggest improvements in grazing management and thus be of future value in the field of nature conservation.

Sixteen permanent sample plots (1 m^2) were selected to follow the changes of vegetation over the years 1975—1977 in open meadows and forest plantations along the three ridges. The cover and phenological aspect of each species were recorded twice a year in each plot. The trend of variations of vegetation in the plots was obviously strongly affected by climatic conditions.

Vegetational changes were less advanced on the Recent ridge. A vegetation close to a "climax", i.e. a *Quercus-Corylus*-wood, has been established earlier on the Litorina than on the Ancylus ridge, though most of the vegetation is still far from mature.

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Table 1. Meteorological data for the study period (1975–1977) at the Sugar Company Meteorological observation post in Mörbylånga, Öland (5 m above sea level), situated at a minimum distance of about 7 km south of the study area.

year T temperature 13.h (°C) R = precipitation (mm) S = snow fall (days)	1975					1976					1977				
	T max.	T min.	T mean	R	S	T max.	T min.	T mean	R	S	T max.	T min.	T mean	R	S
month:															
Januari	8.3	-2.2	4.0	37.3	5	5.6	-8.4	-1.0	32.9	8	2.4	-3.9	0.2	57.7	12
February	9.4	-3.8	2.9	4.5	.	8.2	-5.0	0.3	5.6	5	2.9	-5.1	-0.4	38.1	4
March	8.1	-0.4	3.8	30.2	4	5.9	-4.1	0.6	35.9	18	8.9	-1.1	3.3	28.3	3
April	17.6	2.9	7.9	20.5	5	15.2	1.9	6.3	46.4	6	10.2	-2.2	5.1	20.9	1
May	20.2	7.4	13.1	60.4	2	19.5	4.8	13.6	45.3	.	18.7	8.9	13.0	23.7	.
June	23.6	8.5	17.2	4.5	.	25.8	11.3	17.3	44.5	.	25.8	9.8	17.7	23.9	.
July	25.3	17.2	21.0	15.2	.	24.8	13.2	20.1	33.8	.	25.3	12.0	17.7	79.7	.
August	29.9	17.1	23.2	27.6	.	24.5	16.4	20.0	38.6	.	21.9	16.0	18.8	26.8	.
September	23.6	14.2	17.8	48.8	.	18.9	8.6	14.1	39.5	.	20.2	9.9	14.2	25.9	.
October	15.2	6.6	10.7	34.3	.	14.6	3.2	8.1	29.3	.	14.0	7.3	10.8	24.2	.
November	10.8	-1.4	5.6	25.7	2	9.6	-0.4	5.6	19.0	1	11.0	-0.3	6.2	65.1	6
December	7.1	-1.8	3.8	4.2	2	6.0	-9.1	-0.2	107.6	14	7.8	-2.8	2.4	61.8	4
mean temp. °C and total ppt.	16.6	5.4	10.9	313.2	20	14.9	2.7	8.7	478.4	52	14.1	4.0	9.1	476.1	30

Table 2. General composition of vegetation on the Ancylus, Litorina and Recent ridge (A, L, R). Maximum and mean cover values (c) of the species in the tree-shrub and field layer on each ridge. Percentage presence (p) in stands of the individual ridges and in all stands (P_t). Maximum values underlined.

ridge	A			L			R			
presence and cover (%)	p	c		p	c		p	c		P_t
		max.	mean		max.	mean		max.	mean	
tree and shrub layer:										
Quercus robur	17	65.0	3.40	91	74.7	30.70	14	7.0	0.80	38
Corylus avellana	37	86.0	5.90	64	80.0	20.70	.	.	.	34
Juniperus communis	10	11.3	0.60	46	6.8	0.80	33	30.0	2.60	27
Betula verrucosa	13	75.0	2.50	68	78.0	11.80	5	34.3	1.60	27
Sorbus aucuparia	30	52.9	4.20	36	1.7	0.80	.	.	.	23
Ribes alpinum	23	6.8	0.80	23	1.7	0.20	5	0.3	0.01	18
Rosa spp.	10	5.0	0.20	14	1.0	0.07	29	1.3	0.20	16
Fraxinus excelsior	23	16.9	1.50	23	13.7	1.30	.	.	.	16
Pinus sylvestris	27	70.0	12.20	5	4.7	0.20	14	66.3	6.00	16
Prunus spinosa	23	94.0	3.80	14	11.7	0.60	.	.	.	14
Crataegus sp.	3	5.0	0.20	23	0.7	0.10	.	.	.	8
Lonicera xylosteum	3	2.0	0.07	23	0.7	0.10	.	.	.	8
Rhamnus frangula	10	5.0	0.20	18	1.7	0.20	.	.	.	8
Acer platanoides	13	3.8	0.30	.	.	.	.	.	.	6
Euconymus europaeus	7	0.9	0.03	5	0.3	0.01	.	.	.	4
Malus sylvestris	.	.	.	5	0.3	0.01	10	1.0	0.07	4
Populus tremula	3	6.3	0.20	5	0.7	0.03	.	.	.	3
Sorbus intermedia	7	0.9	0.04	.	.	.	.	.	.	3
Alnus glutinosa	.	.	.	5	21.0	1.00	.	.	.	1
Salix cinerea	.	.	.	5	2.7	0.10	.	.	.	1
field layer:										
Galium verum	80	36.6	8.90	46	9.0	1.50	95	22.0	6.70	74
Poa angustifolia	87	38.3	8.60	59	17.0	3.40	71	8.5	1.70	74
Campanula rotundifolia	77	7.8	1.50	55	5.2	0.60	91	7.8	2.20	73
Agrostis tenuis	83	26.0	8.60	46	14.8	2.30	81	11.8	4.50	72
Veronica chamaedrys	87	22.0	6.10	82	9.8	2.50	38	9.50	0.70	72
Achillea millefolium	80	11.9	2.90	36	13.7	2.10	91	15.7	6.30	70
Deschampsia flexuosa	50	11.2	1.70	73	33.2	9.20	67	67.8	9.10	62
Festuca ovina	63	43.9	7.40	27	11.8	1.40	91	29.3	13.50	60
Viola riviniana	63	14.5	1.30	90	9.5	2.90	24	0.5	0.07	60
Luzula campestris	57	8.3	1.30	32	8.8	1.20	91	8.8	2.10	58
Plantago lanceolata	63	12.6	2.50	23	10.2	0.90	91	11.3	3.40	58
Anthoxanthum odoratum	67	24.8	3.20	46	5.8	0.90	52	2.0	0.30	56
Phleum phleoides	80	17.3	4.90	14	4.0	0.30	57	8.7	2.00	53
Rumex acetosa	50	10.1	1.00	50	3.8	0.30	52	6.5	1.00	51
Anemone pratensis	63	16.0	1.70	27	2.0	0.30	52	6.5	1.70	49
Melampyrum pratense	50	25.4	4.10	86	18.2	5.20	10	9.5	0.50	49
Allium vineale	53	1.6	0.30	40	8.0	1.10	48	7.0	1.20	48
Arrhenatherum pratense	63	20.0	5.20	18	8.3	0.70	52	6.3	0.60	47
Knautia arvensis	77	6.7	1.40	36	3.5	0.50	14	6.7	0.40	47
Quercus robur	43	6.1	1.10	64	2.8	0.90	33	3.0	0.30	47
Hieracium pilosella	40	17.3	1.70	14	5.0	0.30	91	11.5	4.40	45
Hypericum perforatum	67	4.8	1.00	36	3.5	0.60	24	10.8	0.70	45
Arrhenatherum pubescens	50	28.0	2.90	40	9.7	0.90	33	4.7	0.50	43
Convallaria majalis	40	32.9	3.30	77	68.0	11.30	10	9.8	0.80	43
Festuca rubra	57	16.1	2.30	23	7.2	0.50	43	8.8	1.60	43
Fraxinus excelsior	60	10.9	2.30	59	18.7	2.20	.	.	.	43
Potentilla tabernaemontani	47	11.8	1.50	9	4.7	0.30	67	8.3	2.50	41
Silene nutans	47	7.0	0.90	9	1.3	0.07	67	5.3	1.10	41
Stellaria holostea	43	15.9	2.80	68	26.3	6.40	5	0.2	0.01	40
Dactylis glomerata	67	15.3	3.50	32	16.2	1.30	5	0.2	0.01	38
Rumex acetosella	30	2.7	0.20	5	0.7	0.03	81	13.7	3.60	37
Veronica spicata	40	14.9	2.00	14	11.0	0.50	57	7.5	2.10	37
Hepatica nobilis	43	25.6	2.70	64	22.7	6.80	.	.	.	37
Thymus serpyllum	30	18.2	2.50	18	1.0	0.09	62	52.3	5.60	36
Fragaria vesca	53	31.0	2.30	46	3.2	0.40	.	.	.	36
Stellaria graminea	37	23.3	1.40	9	0.5	0.03	57	17.3	2.30	34
Melica nutans	30	3.7	0.30	73	26.8	4.60	.	.	.	34
Prunus spinosa	57	45.3	3.60	18	5.8	0.40	14	2.8	0.20	33
Trifolium campestre	33	6.5	0.70	9	3.0	0.20	57	3.5	0.80	33
Viscaria vulgaris	27	3.1	0.20	9	1.5	0.10	67	35.3	3.10	33
Rosa spp.	33	2.2	0.20	36	1.8	0.30	24	20.5	1.90	32
Saxifraga granulata	30	2.2	0.30	18	6.2	0.40	48	4.7	0.50	32
Carex caryophyllea	30	2.8	0.30	18	2.0	0.20	43	3.3	0.60	30
Luzula pilosa	27	7.9	0.80	55	5.8	1.20	10	0.5	0.03	30
Ranunculus bulbosus	37	2.8	0.40	5	2.3	0.10	48	4.0	0.80	30
Ribes alpinus	40	4.6	1.00	40	1.3	0.30	5	1.3	0.06	30
Lathyrus montanus	23	4.0	0.30	59	3.8	1.00	5	0.7	0.03	29
Anemone nemorosa	13	12.0	0.90	77	32.3	11.00	.	.	.	29
Geum urbanum	50	8.4	1.10	27	1.5	0.20	.	.	.	29
Primula veris	37	5.4	0.50	46	4.0	0.70	.	.	.	29
Sedum acre	33	17.5	2.00	.	.	.	52	9.0	1.90	29
Lotus corniculatis	17	2.2	0.10	9	0.2	0.02	62	8.0	1.50	27
Sorbus aucuparia	43	13.4	1.20	27	0.7	0.10	5	1.7	0.08	27
Armeria maritima	17	1.1	0.08	.	.	.	71	6.3	1.60	27
Calluna vulgaris	20	39.7	2.10	14	65.7	5.40	48	49.3	8.70	26
Cerastium brachypetalum	23	11.0	0.70	5	1.0	0.05	52	7.3	1.00	26
Veronica officinalis	27	4.1	0.40	18	1.0	0.10	33	1.2	0.20	26
Galium aparine	37	13.7	1.10	27	1.2	0.10	5	1.5	0.07	25
Helianthemum nummularium	33	20.9	1.20	18	37.7	2.00	19	20.7	1.60	25
Mercurialis perennis	33	22.3	1.40	36	54.0	4.10	.	.	.	25
Trifolium montanum	23	1.1	0.40	14	2.8	0.20	33	1.5	0.80	23
Veronica arvensis	23	4.7	0.30	5	2.3	0.10	43	2.3	0.50	23
Dianthus deltoides	20	3.6	0.20	.	.	.	52	1.0	0.30	23
Galium boreale	10	23.2	0.80	23	8.5	0.70	38	5.3	1.80	22
Taraxacum spp. (Vulg.)	13	0.4	0.04	9	6.7	0.40	48	3.7	0.90	22

Table 2. (contin.)

ridge	A			L			R			P_t
presence and cover (%)	p	c		p	c		p	c		
		max.	mean		max.	mean		max.	mean	
field layer (contin.):										
Poa nemoralis	30	36.9	3.00	32	11.0	1.00	.	.	.	22
Anthriscus sylvestris	30	33.2	2.30	23	25.1	1.50	5	1.0	0.50	21
Rubus saxatilis	23	52.1	2.90	32	5.5	0.80	5	0.8	0.04	21
Corylus avellana	30	3.2	0.40	27	1.3	0.20	.	.	.	21
Pimpinella saxifraga	20	4.0	0.20	9	0.2	0.02	29	7.8	0.70	19
Sesleria coerulea ssp.ulig.	7	2.4	0.10	23	2.8	0.40	33	9.3	4.90	19
Adoxa moschatellina	17	2.7	0.20	40	1.5	0.30	.	.	.	19
Laserpitium latifolium	23	3.9	0.40	32	19.0	1.10	.	.	.	19
Arrhenatherum elatius	27	54.5	4.30	18	45.3	2.50	5	0.5	0.02	18
Vicia cracca	7	2.5	0.10	27	14.9	0.80	24	4.0	0.30	18
Maianthemum bifolium	23	8.3	0.70	27	31.7	2.80	.	.	.	18
Oxalis acetosella	20	25.0	1.10	32	28.0	2.20	.	.	.	18
Pulmonaria officinalis	7	0.8	0.04	50	2.7	0.60	.	.	.	18
Potentilla argentea	13	0.4	0.04	.	.	.	43	1.7	0.30	18
Ranunculus auricomus (coll.)	7	3.3	0.10	46	2.5	0.50	.	.	.	16
Trifolium medium	13	41.5	2.70	36	43.7	3.00	.	.	.	16
Trifolium arvense	10	3.6	0.10	.	.	.	43	2.7	0.40	16
Moehringia trinervia	40	12.2	1.20	.	.	.	.	.	.	16
Filipendula vulgaris	20	12.7	0.80	14	9.8	0.80	10	0.5	0.05	15
Vicia hirsuta	13	18.1	0.60	5	2.3	0.10	29	0.5	0.07	15
Hypericum maculatum	7	3.4	0.10	40	2.7	0.40	.	.	.	15
Polygonatum multiflorum	27	1.4	0.20	14	1.0	0.09	.	.	.	15
Roegneria canina	37	13.8	1.30	.	.	.	.	.	.	15
Bromus hordeaceus	3	0.7	0.02	5	0.5	0.02	38	19.7	1.10	14
Juniperus communis	7	1.4	0.07	5	1.2	0.05	33	2.3	0.40	14
Lonicera xylosteum	13	3.1	0.30	27	2.0	0.40	.	.	.	14
Scorzonera humilis	10	0.9	0.05	32	0.7	0.10	.	.	.	14
Serratula tinctoria	17	4.7	0.40	23	8.8	0.60	.	.	.	14
Artemisia campestris	27	9.1	0.70	.	.	.	10	1.5	0.10	14
Carex hirta	.	.	.	9	1.8	0.10	38	9.7	0.90	14
Carex arenaria	.	.	.	.	.	.	48	59.5	5.50	14
Centaurea scabiosa	17	0.5	0.05	18	6.2	0.60	.	.	.	12
Rubus caesius	27	30.3	1.60	5	0.2	0.01	.	.	.	12
Euphrasia spp.	7	0.8	0.04	.	.	.	33	1.5	0.03	12
Trifolium pratense	3	5.7	0.20	.	.	.	38	6.5	1.30	12
Viola hirta	.	.	.	40	7.0	0.80	.	.	.	12
Melampyrum sylvaticum	7	0.5	0.03	27	7.2	0.60	.	.	.	11
Populus tremula	20	29.3	1.60	9	17.8	0.90	.	.	.	11
Aira praecox	3	0.1	<0.01	5	0.8	0.04	24	9.0	1.10	10
Briza media	7	1.4	0.06	5	0.3	0.01	19	8.3	0.60	10
Campanula persicifolia	3	1.3	0.04	27	10.1	0.90	.	.	.	10
Geranium robertianum	20	9.4	0.60	5	0.8	0.04	.	.	.	10
Rubus idaeus	20	19.3	1.00	5	6.0	0.30	.	.	.	10
Hypochoeris maculata	17	1.3	0.10	.	.	.	10	0.5	0.03	10
Myosotis stricta	17	0.5	0.05	.	.	.	10	0.2	0.01	10
Poa compressa	3	0.1	<0.01	.	.	.	29	0.5	0.08	10
Chamaenerion angustifolium	23	1.6	0.20	.	.	.	.	.	.	10
Potentilla erecta	.	.	.	18	1.0	0.10	14	2.2	0.20	10
Dentaria bulbifera	.	.	.	32	20.2	2.10	.	.	.	10
Hypochoeris radicata	.	.	.	.	.	.	33	2.3	0.30	10
Sedum maximum	.	.	.	.	.	.	33	3.5	0.40	10
Alchemilla spp.	7	1.1	0.05	9	0.2	0.30	10	0.5	0.03	8
Carex pallescens	13	1.3	0.08	5	6.3	0.30	5	0.2	0.01	8
Carex pilulifera	13	0.6	0.04	5	0.3	0.01	5	0.2	0.01	8
Erophila verna	10	1.2	0.05	5	0.3	0.01	10	2.0	0.10	8
Aegopodium podagraria	3	0.5	0.02	23	44.8	4.60	.	.	.	8
Pteridium aquilinum	10	27.9	1.10	14	20.5	1.10	.	.	.	8
Valeriana officinalis	7	1.9	0.10	18	0.5	0.05	.	.	.	8
Antennaria dioica	3	0.2	0.01	.	.	.	24	3.3	0.40	8
Scleranthus annuus	7	0.3	0.01	.	.	.	19	2.3	0.20	8
Polygala vulgaris	13	0.3	0.02	.	.	.	10	0.5	0.04	8
Melampyrum cristatum	20	7.4	0.70	.	.	.	.	.	.	8
Plantago maritima	.	.	.	.	.	.	29	3.0	0.30	8
Vicia lathyroides	7	0.4	0.02	5	2.8	0.10	10	3.7	0.20	7
Dactylorhiza sambucina	13	0.6	0.03	5	6.2	0.30	.	.	.	7
Hieracium sylvaticum	10	0.8	0.05	9	1.8	0.10	.	.	.	7
Milium effusum	10	7.2	0.30	9	2.5	0.20	.	.	.	7
Myosotis ramosissima	10	3.5	0.10	9	0.5	0.04	.	.	.	7
Solidago virgaurea	7	1.4	0.06	14	0.8	0.06	.	.	.	7
Trifolium repens	3	0.2	0.01	.	.	.	19	3.7	0.20	7
Euonymus europaeus	17	1.3	0.10	.	.	.	.	.	.	7
Hieracium sp.	.	.	.	9	2.3	0.10	14	0.5	0.06	7
Rhamnus frangula	7	2.6	0.10	9	1.0	0.06	.	.	.	6
Arabidopsis thaliana	.	.	.	9	0.8	0.05	10	2.8	0.10	6
Anemone ranunculoides	.	.	.	18	2.0	0.20	.	.	.	6
Melica uniflora	.	.	.	18	22.7	1.50	.	.	.	6
Viburnum opulus	.	.	.	18	0.8	0.10	.	.	.	6
Puccinellia distans	.	.	.	.	.	.	19	1.0	0.10	6
Crataegus sp.	7	2.5	0.10	5	0.2	0.01	.	.	.	4
Equisetum arvense	7	1.4	0.06	.	.	.	5	0.3	0.01	4
Turrtis glabra	7	0.3	0.01	.	.	.	5	1.2	0.06	4
Anthyllis vulneraria	10	0.3	0.02	.	.	.	.	.	.	4
Carex divulsa	10	2.3	0.10	.	.	.	.	.	.	4
Equisetum hyemale	10	1.3	0.09	.	.	.	.	.	.	4
Dryopteris filix-mas	10	0.7	0.05	.	.	.	.	.	.	4
Vicia tetrasperma	10	2.0	0.10	.	.	.	.	.	.	4
Chrysanthemum vulgare	10	8.8	0.40	.	.	.	.	.	.	4
Equisetum sp.	.	.	.	5	0.8	0.04	10	0.3	0.02	4
Geranium sanguineum	.	.	.	14	43.3	4.20	.	.	.	4
Holcus lanatus	.	.	.	14	2.2	0.10	.	.	.	4
Sieglingia decumbens	.	.	.	.	.	.	14	1.2	0.08	4

Table 2. (contin.)

ridge	A			L			R			P_t
presence and cover (%)	p	c		p	c		p	c		
		max.	mean		max.	mean		max.	mean	
field layer (contin.):										
Brachypodium sylvaticum	3	0.7	0.02	5	3.3	0.20	.	.	.	3
Epipactis helleborine	3	0.4	0.01	5	0.2	0.01	.	.	.	3
Geranium sylvaticum	3	0.5	0.02	5	4.0	0.20	.	.	.	3
Urtica urens	3	0.4	0.01	5	0.2	0.01	.	.	.	3
Arenaria serpyllifolia	3	0.4	0.01	.	.	.	5	0.3	0.01	3
Matricaria inodora	3	0.3	0.01	.	.	.	5	0.1	0.05	3
Geranium molle	3	0.5	0.02	.	.	.	5	0.3	0.01	3
Carex ericetorum	7	0.7	0.03	.	.	.	.	.	.	3
Jasione montana	7	2.3	0.08	.	.	.	.	.	.	3
Lactuca muralis	7	0.1	0.01	.	.	.	.	.	.	3
Linaria vulgaris	7	2.0	0.10	.	.	.	.	.	.	3
Sanicula europaea	7	2.3	0.09	.	.	.	.	.	.	3
Succisa pratensis	7	0.5	0.03	.	.	.	.	.	.	3
Luzula multiflora	.	.	.	5	2.3	0.10	5	0.8	0.04	3
Carex sylvatica	.	.	.	9	0.5	0.03	.	.	.	3
Filipendula ulmaria	.	.	.	9	0.7	0.04	.	.	.	3
Listera ovata	.	.	.	9	1.0	0.06	.	.	.	3
Carex nigra	.	.	.	.	.	.	10	2.8	0.10	3
Lolium perenne	.	.	.	.	.	.	10	3.7	0.30	3
Acer platanoides	3	0.6	0.02	.	.	.	.	.	.	1
Agrimonia eupatoria	3	0.4	0.01	.	.	.	.	.	.	1
Betula verrucosa	3	1.2	0.04	.	.	.	.	.	.	1
Carex distans	3	7.6	0.30	.	.	.	.	.	.	1
Carex flacca	3	0.2	0.01	.	.	.	.	.	.	1
Cerastium semidecandrum	3	0.3	0.01	.	.	.	.	.	.	1
Erigeron acer	3	0.2	0.01	.	.	.	.	.	.	1
Medicago falcata	3	0.8	0.03	.	.	.	.	.	.	1
Polygonum convolvolus	3	0.9	0.03	.	.	.	.	.	.	1
Prunus avium	3	3.9	0.10	.	.	.	.	.	.	1
Rubus corylifolius (coll.)	3	2.3	0.08	.	.	.	.	.	.	1
Sambucus nigra	3	0.1	<0.01	.	.	.	.	.	.	1
Sorbus intermedia	3	0.3	0.01	.	.	.	.	.	.	1
Stellaria media	3	0.2	0.01	.	.	.	.	.	.	1
Ulmus glabra	3	0.7	0.02	.	.	.	.	.	.	1
Chrysanthemum leucanthemum	.	.	.	5	1.0	0.05	.	.	.	1
Dactylorhiza maculata	.	.	.	5	1.7	0.08	.	.	.	1
Geum rivale	.	.	.	5	3.3	0.20	.	.	.	1
Hedera helix	.	.	.	5	0.7	0.03	.	.	.	1
Lathyrus pratensis	.	.	.	5	2.3	0.10	.	.	.	1
Lysimachia vulgaris	.	.	.	5	4.5	0.20	.	.	.	1
Orchis mascula	.	.	.	5	0.2	0.01	.	.	.	1
Phleum pratense	.	.	.	5	1.2	0.06	.	.	.	1
Tussilago farfara	.	.	.	5	0.3	0.01	.	.	.	1
Viola mirabilis	.	.	.	5	1.0	0.05	.	.	.	1
Cirsium acaule	.	.	.	.	.	.	5	5.5	0.30	1
Cynosurus cristatus	.	.	.	.	.	.	5	5.2	0.30	1
Galium palustre	.	.	.	.	.	.	5	0.5	0.02	1
Peucedanum oreoselinum	.	.	.	.	.	.	5	2.8	0.10	1
Potentilla reptans	.	.	.	.	.	.	5	0.2	0.01	1
Prunella grandiflora	.	.	.	.	.	.	5	0.2	0.01	1
Ranunculus acris	.	.	.	.	.	.	5	4.2	0.20	1
Viola arvensis	.	.	.	.	.	.	5	0.2	0.01	1
bottom layer:										
Mnium affine	60	.	.	55	.	.	38	.	.	52
Dicranum scoparium	10	.	.	18	.	.	86	.	.	34
Pleurozium schreberi	33	.	.	32	.	.	33	.	.	33
Rhytidiadelphus squarrosus	37	.	.	9	.	.	43	.	.	30
Brachythecium albicans	30	.	.	5	.	.	48	.	.	27
Brachythecium rutabulum	47	.	.	18	.	.	10	.	.	27
Hypnum cupressiforme	23	.	.	.	.	.	52	.	.	25
Rhodobryum roseum	27	.	.	23	.	.	14	.	.	22
Abietinella abietina	23	.	.	.	.	.	29	.	.	18
Cladonia sp.	7	.	.	.	.	.	38	.	.	14
Hylocomium splendens	10	.	.	5	.	.	24	.	.	12
Cirrphyllum piliferum	17	.	.	.	.	.	14	.	.	11
Polytrichum juniperinum	.	.	.	5	.	.	33	.	.	11
Climacium dendroides f.lep.	7	.	.	5	.	.	19	.	.	10
Brachythecium velutinum	17	.	.	9	.	.	.	.	.	10
Pseudosderopodium purum	13	.	.	5	.	.	.	.	.	7
Ceratodon purpureus	7	.	.	.	.	.	14	.	.	7
Tortula ruralis	3	.	.	.	.	.	19	.	.	7
Dicranum polysetum	3	.	.	.	.	.	10	.	.	6
Camptothecium lutescens	13	.	.	.	.	.	.	.	.	6
Pohlia nutans	7	.	.	.	.	.	5	.	.	4
Brachythecium salebrosum	10	.	.	.	.	.	.	.	.	4
Eurhynchium praelongum	10	.	.	.	.	.	.	.	.	4
Lophocolea heterophylla	10	.	.	.	.	.	.	.	.	4
Brachythecium populeum	3	.	.	5	.	.	.	.	.	3
Plagiothecium sylvaticum	3	.	.	.	.	.	5	.	.	3
Brachythecium sp.	3	.	.	5	.	.	.	.	.	3
Bryum sp.	7	.	.	.	.	.	.	.	.	3
Rhytidiadelphus triquetrus	7	.	.	.	.	.	.	.	.	3
Mnium undulatum	.	.	.	9	.	.	.	.	.	3
Bryum capillare	.	.	.	.	.	.	10	.	.	3
Amblystegium serpens	3	.	.	.	.	.	.	.	.	1
Peltigera canina	3	.	.	.	.	.	.	.	.	1
Eurhynchium striatum	.	.	.	5	.	.	.	.	.	1
Polytrichum commune	.	.	.	5	.	.	.	.	.	1
Aulacomnium androgynum	.	.	.	.	.	.	5	.	.	1
Cornicularia aculeata	.	.	.	.	.	.	5	.	.	1

Table 3. Variations in factors affecting the microclimate (relative light, vegetation moisture index, and canopy cover) between the stands. Figures in parentheses show the number of light measurements.

	light (lux 10^3)			rel.	moist.	tree-shrub
	range	mean	SD	light (%)	index	cover sum (%)
Ancylus						
1	11.0-14.5	12.94(10)	1.29	89	2	.
2	14.5-14.5	14.50(5)	.	100	2	.
3	14.5-14.5	14.50(5)	.	100	1	.
4	14.5-14.5	14.50(5)	.	100	2	.
5	14.5-14.5	14.50(5)	.	100	1	.
6	11.0-15.6	12.68(5)	1.38	81	3	.
7	2.4-15.6	3.19(10)	0.60	20	4	135.0
8	11.8-12.6	11.80(5)	.	94	1	.
9	2.8-12.6	6.41(5)	1.85	51	3	0.6
10	0.7-12.6	0.83(7)	0.10	07	4	185.0
11	5.2-11.8	7.52(6)	1.58	64	3	100.3
12	7.8-13.5	9.77(6)	1.10	72	3	.
13	5.2-13.5	5.67(9)	0.44	42	3	3.0
14	2.6-13.5	3.94(10)	0.99	29	4	148.0
15	2.6-12.6	3.30(9)	0.34	26	3	63.0
16	8.4-22.0	9.45(8)	0.67	43	3	25.0
17	7.8-17.9	10.38(8)	2.18	58	4	65.5
18	1.6-13.5	3.38(10)	1.55	25	4	98.4
19	3.4-13.5	4.30(10)	0.86	32	4	59.7
20	11.0-14.5	13.22(5)	1.47	91	2	11.3
21	3.4-11.8	6.63(8)	2.79	56	3	2.1
22	11.0-11.8	11.00(5)	.	93	1	0.2
23	3.7-12.6	5.20(10)	0.75	41	4	70.7
24	6.0-12.6	6.58(8)	0.41	52	3	11.4
25	2.8-13.5	3.12(8)	0.41	23	4	85.0
26	1.6-13.5	2.04(9)	0.24	15	4	130.4
27	3.0-13.5	6.38(10)	3.00	47	3	.
28	4.9-13.5	8.06(8)	2.08	60	3	.
29	4.9-12.6	7.89(10)	2.01	63	3	1.1
30	5.6-12.6	10.10(10)	2.67	80	1	0.4
Litorina						
1	25.1-25.1	25.10(5)	.	100	2	.
2	4.9-11.0	7.44(12)	3.70	68	3	43.7
3	8.4-11.0	9.66(7)	1.07	88	2	8.4
4	6.0- 9.6	6.90(7)	0.69	72	3	13.6
5	2.1- 9.6	2.53(10)	0.43	26	4	79.3
6	15.6-16.7	10.23(11)	1.70	61	2	21.4
7	2.6- 9.6	3.07(7)	0.35	32	5	63.7
8	10.3-16.7	13.64(13)	1.72	82	2	7.5
9	10.3-16.7	11.52(11)	0.88	69	2	13.0
10	7.3-23.5	8.93(6)	0.97	38	3	54.6
11	3.7-11.0	6.28(14)	1.60	57	3	65.3
12	3.9-11.0	4.80(11)	1.17	44	3	57.5
13	2.1-11.0	2.32(7)	0.12	21	4	72.4
14	1.2-11.8	1.57(12)	0.24	13	4	108.4
15	0.7-11.8	0.90(8)	0.13	8	4	140.3
16	1.1-11.8	1.37(12)	0.64	16	4	135.0
17	2.3-11.8	2.96(13)	0.51	25	3	90.4
18	1.4-11.8	1.70(9)	0.23	14	4	127.0
19	0.8-11.8	1.25(13)	0.36	11	4	144.4
20	0.5-11.0	0.67(10)	0.20	6	4	145.1
21	4.6-13.5	5.67(13)	1.32	42	3	54.3
22	1.4-11.8	2.35(8)	0.64	20	3	66.0
Recent						
1	13.5-14.5	13.50(5)	.	93	2	.
2	10.3-14.5	12.83(10)	1.07	89	2	.
3	2.6-14.5	3.06(9)	0.35	21	4	46.6
4	1.3-14.5	1.40(7)	0.10	10	4	73.3
5	31.0-31.0	31.00(5)	.	100	1	.
6	15.6-31.0	22.70(10)	4.55	73	3	5.6
7	9.6-31.0	15.49(10)	3.94	50	4	32.0
8	31.0-31.0	31.00(5)	.	100	1	.
9	31.0-31.0	31.00(5)	.	100	1	.
10	27.0-31.0	30.20(10)	1.40	97	3	.
11	31.0-31.0	31.00(5)	.	100	1	.
12	2.5-31.0	30.21(10)	1.90	98	2	1.7
13	17.9-31.0	27.55(10)	4.21	89	3	7.0
14	31.0-31.0	31.00(5)	.	100	1	.
15	31.0-31.0	31.00(5)	.	100	1	.
16	16.7-31.0	26.49(10)	4.47	86	3	6.7
17	29.0-31.0	29.00(5)	.	94	3	.
18	2.8-19.0	4.74(16)	1.72	25	4	64.0
19	16.7-19.0	18.25(6)	0.93	96	1	.
20	16.7-19.0	16.70(5)	.	88	3	.
21	17.9-19.0	17.90(5)	.	94	2	.

Table 4a. Soil analysis in the Ancylus ridge stands. Surface horizon (H_0) and horizon below (H_1). Minimum values are underlined by a single solid (H_0) or dotted (H_1) line, maximum values by a double solid (H_0) or dashed (H_1) line. Comparation of amount of variation in each soil factor by coefficient of variation (CV = SD/MEAN • 100). Conductivity (cond.) as µmhos/cm.

no. of stand	horizon	soil depth (cm)	soil H.M. (%)	water W.H.C. (%)	chemical properties O.M. (%)	Ntot (%)	pH	cond.	C.E.C.	T.E.B.	T.A.	K^+	Na^+	Mg^{2+}	Ca^{2+} (meq./100 g)	texture (%) part. >2 mm	sand	sand coarse	fract. med.	fine	silt	clay
1	H_0	>30	0.3	40.7	5.0	0.17	5.6	124.0	7.1	3.1	4.0	0.2	0.03	0.5	2.5	0.9	94	17.1	61.8	19.2	4	2
	H_1		0.5	26.1	2.0	0.17	5.6	51.4	3.8	0.9	2.9	0.1	0.02	0.1	0.7	2.2	98	14.5	61.4	22.9	2	0
2	H_0	"	0.7	30.2	2.8	0.17	5.6	102.1	7.9	2.7	5.2	0.1	0.03	0.4	2.2	1.2	94	16.9	60.4	19.4	4	2
	H_1		0.5	28.7	2.4	0.07	5.6	39.1	5.8	1.2	4.6	0.1	0.01	0.1	0.8	4.0	98	19.5	58.8	19.5	2	0
3	H_0	"	1.1	35.5	2.6	0.25	5.7	165.3	.	.	.	.	.	.	.	1.3	96	29.0	56.3	12.1	2	2
	H_1		0.5	26.3	2.6	0.08	5.6	67.8	.	.	.	.	.	.	.	6.4	98	32.1	53.9	11.4	2	0
4	H_0	"	1.8	44.7	5.1	0.21	5.7	165.3	.	.	.	.	.	.	.	3.5	94	23.4	53.3	18.3	4	2
	H_1		0.6	28.3	3.1	0.10	5.6	73.1	.	.	.	.	.	.	.	9.1	96	25.6	55.5	15.0	2	2
5	H_0	9	1.3	55.0	9.2	0.32	5.5	195.6	15.9	7.3	8.6	0.4	0.01	0.9	6.0	32.5	90	29.5	48.7	17.4	8	2
	H_1		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6	H_0	>50	0.9	47.0	6.5	0.19	5.4	182.7	.	.	.	.	.	.	.	4.6	94	22.4	55.1	18.9	4	2
	H_1		0.7	32.5	3.1	0.10	5.3	105.2	.	.	.	.	.	.	.	13.9	94	28.9	51.0	16.4	4	2
7	H_0	"	2.4	96.3	22.1	0.59	5.4	463.0	27.8	20.4	7.4	0.7	0.20	3.7	17.0	2.5	88	43.9	43.2	9.6	6	6
	H_1		1.4	53.6	13.5	0.39	4.5	239.5	20.0	5.3	14.7	0.3	0.10	0.9	4.4	11.5	88	29.4	50.4	14.6	8	4
8	H_0	"	0.9	46.5	6.4	0.26	5.4	131.0	5.3	4.8	0.5	0.2	0.05	0.6	3.6	3.3	94	27.6	52.9	16.4	4	2
	H_1		0.6	26.8	3.2	0.10	5.6	60.4	7.4	1.6	5.8	0.1	0.01	0.2	1.2	20.8	96	29.1	52.4	14.2	2	2
9	H_0	"	1.0	52.2	8.1	0.29	5.0	195.6	.	.	.	.	.	.	.	2.5	92	21.0	58.0	17.1	6	2
	H_1		0.8	22.6	3.4	0.11	5.1	89.0	.	.	.	.	.	.	.	10.5	95	32.8	50.8	13.1	5	0
10	H_0	"	2.0	58.1	11.1	0.35	5.0	239.5	.	.	.	.	.	.	.	0.4	90	24.5	64.1	8.8	8	2
	H_1		0.9	32.6	6.1	0.20	4.9	161.5	.	.	.	.	.	.	.	11.0	92	35.3	52.0	8.6	6	2
11	H_0	"	0.9	41.1	6.5	0.24	5.6	157.7	9.7	5.0	4.7	0.3	0.03	0.7	4.2	0.0	94	9.2	60.7	27.6	4	2
	H_1		0.5	36.6	3.6	0.12	5.4	81.7	5.4	2.0	3.7	0.1	0.01	0.2	1.7	0.9	96	11.4	58.3	28.0	2	2
12	H_0	"	1.5	63.5	8.9	0.30	5.6	190.3	.	.	.	.	.	.	.	0.4	94	9.6	63.3	24.4	4	2
	H_1		0.6	36.0	3.6	0.14	5.6	86.8	.	.	.	.	.	.	.	2.0	96	12.0	58.5	26.5	4	0
13	H_0	"	0.9	48.0	6.8	0.23	5.6	347.2	10.1	5.2	4.7	0.3	0.03	0.9	4.2	0.1	94	10.3	64.8	22.5	4	2
	H_1		0.7	24.6	3.7	0.13	5.2	112.0	6.3	2.0	4.3	0.1	0.03	0.3	1.6	2.0	94	17.6	56.0	23.6	4	2
14	H_0	"	1.0	32.6	6.2	0.15	4.8	147.8	9.3	2.4	6.9	0.1	0.04	0.3	2.0	1.7	96	22.9	57.5	17.8	2	2
	H_1		0.5	19.4	2.2	0.06	5.2	119.7	5.4	0.7	5.0	0.1	0.10	1.0	0.6	8.0	94	22.3	53.7	21.5	4	2
15	H_0	"	1.5	59.7	7.8	0.20	5.6	308.6	.	.	.	.	.	.	.	1.0	92	10.3	55.7	31.1	6	2
	H_1		0.3	29.1	2.1	0.06	5.4	81.7	.	.	.	.	.	.	.	2.0	96	10.5	49.0	38.0	4	0
16	H_0	"	1.1	42.0	7.5	0.16	5.4	267.1	9.4	5.2	4.2	0.2	0.04	0.4	4.3	0.9	96	10.1	53.7	33.9	4	0
	H_1		0.4	26.8	1.6	0.05	5.3	57.9	3.8	1.0	2.8	0.1	0.06	0.1	0.8	1.3	96	9.8	47.8	40.4	4	0
17	H_0	"	1.0	42.2	5.7	0.15	4.7	151.0	8.9	2.7	6.2	0.2	0.04	0.3	2.2	1.0	96	11.5	52.3	34.1	4	0
	H_1		0.5	25.1	2.2	0.05	5.1	64.6	7.4	1.1	6.3	0.1	0.02	0.1	0.8	3.2	96	8.7	46.8	42.1	2	2
18	H_0	"	1.0	39.1	9.6	0.18	4.5	173.6	16.8	3.4	13.4	0.1	0.05	0.5	2.6	0.8	94	11.1	52.9	33.9	4	2
	H_1		0.7	27.4	2.6	0.07	4.0	77.2	5.1	0.9	4.2	0.1	0.02	0.1	0.8	2.6	94	9.3	46.8	41.2	4	2
19	H_0	"	1.1	40.1	6.9	0.16	5.1	157.8	.	.	.	.	.	.	.	0.6	92	14.1	56.7	26.7	6	2
	H_1		0.6	33.1	2.9	0.08	5.2	92.6	.	.	.	.	.	.	.	1.1	96	13.8	51.3	31.6	2	2
20	H_0	"	0.8	43.2	5.8	0.17	5.4	110.2	9.4	3.8	5.6	0.2	0.02	0.6	3.1	2.0	94	24.0	54.4	18.3	4	2
	H_1		0.6	27.4	3.2	0.09	5.4	64.6	9.9	1.7	8.2	0.1	0.05	0.3	1.2	5.4	96	32.5	50.0	14.3	4	0
21	H_0	"	1.0	34.7	6.2	0.21	5.3	147.8	13.3	4.9	8.9	0.2	0.03	0.7	4.0	3.6	94	26.3	52.6	17.6	6	0
	H_1		0.5	20.7	2.4	0.07	5.6	56.7	5.7	2.0	3.7	0.1	0.01	0.3	1.2	10.0	96	29.9	52.4	15.0	4	0
22	H_0	"	1.0	46.8	6.8	0.26	5.5	185.2	.	.	.	.	.	.	.	2.2	94	22.5	55.4	16.4	4	2
	H_1		0.6	29.6	3.2	0.11	5.5	102.1	.	.	.	.	.	.	.	13.8	96	34.7	47.5	14.6	4	0
23	H_0	"	1.2	59.0	8.6	0.18	5.2	182.7	.	.	.	.	.	.	.	2.3	94	19.2	57.6	19.9	4	2
	H_1		0.7	22.1	3.0	0.08	5.3	91.4	.	.	.	.	.	.	.	10.4	94	29.8	47.3	19.2	6	0
24	H_0	"	1.1	38.9	6.2	0.14	4.9	147.6	9.2	2.7	6.5	0.1	0.03	0.3	2.3	3.3	94	19.5	56.9	20.2	6	0
	H_1		0.6	29.3	2.9	0.07	5.0	77.2	4.9	0.9	4.0	0.1	0.02	0.1	0.7	6.6	96	29.8	50.1	16.6	4	0
25	H_0	"	1.2	55.2	10.5	0.23	5.0	235.4	.	.	.	.	.	.	.	0.0	90	9.7	63.2	24.1	6	4
	H_1		0.6	32.0	2.6	0.11	4.7	91.4	.	.	.	.	.	.	.	1.7	94	14.2	56.0	26.4	4	2
26	H_0	"	2.0	58.0	16.3	0.42	4.5	239.5	26.2	8.3	18.0	0.3	0.10	1.4	6.9	0.8	84	19.3	60.2	17.7	8	8
	H_1		1.1	31.8	7.4	0.17	4.4	133.5	12.3	1.9	10.4	0.1	0.01	0.3	1.2	7.4	88	20.0	56.2	19.1	8	4
27	H_0	"	1.2	43.5	7.5	0.23	6.0	243.7	12.8	7.7	5.1	0.2	0.01	1.0	6.4	0.1	92	13.6	59.2	24.9	6	2
	H_1		0.8	32.7	3.2	0.13	5.3	106.8	7.5	2.5	5.0	0.2	0.20	0.4	1.6	0.7	98	19.2	53.4	24.6	2	0
28	H_0	"	1.1	41.3	5.9	0.20	6.7	450.9	.	.	.	.	.	.	.	0.0	94	10.3	61.1	26.3	4	2
	H_1		0.5	30.2	3.0	0.11	5.8	110.2	.	.	.	.	.	.	.	1.0	94	14.8	55.9	27.3	4	2
29	H_0	"	1.2	49.2	7.4	0.25	5.7	192.9	.	.	.	.	.	.	.	0.0	94	12.3	61.7	23.6	4	2
	H_1		0.6	34.1	3.6	0.14	5.4	96.5	.	.	.	.	.	.	.	1.1	94	14.2	57.7	25.7	4	2
30	H_0	"	1.0	33.5	6.7	0.24	5.6	187.7	.	.	.	.	.	.	.	1.8	94	20.8	55.9	19.5	6	0
	H_1		0.6	19.9	3.3	0.11	5.5	81.7	.	.	.	.	.	.	.	7.2	94	30.6	50.6	14.6	6	0
$\bar{X}$	H_0		1.2	46.3	7.8	0.24	5.4	206.3	12.5	5.6	6.9	0.24	0.05	0.8	4.6	2.5	93.1	18.7	57.0	21.3	4.9	2.1
	H_1		0.6	29.2	3.5	0.11	5.3	92.2	7.4	1.7	5.7	0.12	0.05	0.2	1.3	6.0	94.9	21.8	52.8	22.3	3.9	1.1
CV	H_0		33.3	27.7	47.4	37.5	9.3	42.4	51.2	78.6	59.4	62.5	100.0	100.0	80.4	232.0	2.8	43.3	8.4	31.0	30.6	76.2
	H_1		33.3	22.6	62.9	63.6	5.7	41.8	55.4	64.7	56.1	50.0	100.0	100.0	69.2	85.0	2.5	41.3	7.6	41.7	43.6	118.2

Table 4b. Soil analysis in the Litorina ridge stands (cf. Table 4a).

no. of stand	horizon	soil depth (cm)	soil H.M. (%)	water W.H.C. (%)	O.M. (%)	Ntot (%)	pH	cond.	C.E.C	T.E.B.	T.A.	K^+ meq./100 g	Na^+	Mg^{2+}	Ca^{2+}	texture (%) part. >2 mm	sand	sand coarse	fract. med.	fine	silt	clay
1	H_0	21	1.2	54.1	9.6	0.41	4.9	169.4	22	11	11	0.10	0.04	1.3	8.8	24.4	84	45.9	34.7	14.0	14	2
	H_1		1.1	27.3	4.9	0.08	5.2	69.4	6	3	4	<0.01	<0.01	0.1	1.6	40.5	90	63.5	26.2	6.3	8	2
2	H_0	19	1.0	55.4	9.3	0.28	5.2	195.6	15	8	7	0.05	0.04	0.9	6.9	35.7	88	47.9	35.6	11.1	12	0
	H_1		0.6	32.7	3.4	0.09	5.0	103.6	6	2	3	<0.01	<0.01	0.1	1.4	48.4	92	53.3	33.4	6.7	8	0
3	H_0	29	1.4	55.0	10.5	0.33	5.1	195.6	.	.	.	.	.	.	.	57.7	92	49.4	38.0	8.4	6	2
	H_1		1.2	30.5	6.3	0.22	5.1	169.4	.	.	.	.	.	.	.	78.5	90	43.3	40.9	9.1	10	0
4	H_0	37	0.9	39.5	6.7	0.20	5.5	128.6	.	.	.	.	.	.	.	28.9	90	52.0	38.6	6.1	8	2
	H_1		0.6	25.3	3.9	0.11	5.3	77.2	.	.	.	.	.	.	.	30.3	94	51.9	39.1	5.2	6	0
5	H_0	22	1.7	48.8	8.9	0.23	5.0	161.5	15	7	8	0.05	0.04	0.9	5.0	57.0	88	40.6	47.1	8.7	10	2
	H_1		1.1	31.5	5.0	0.14	4.6	99.2	10	2	7	<0.01	<0.01	0.2	1.6	64.7	92	39.9	43.9	9.7	8	0
6	H_0	30	0.8	43.1	6.5	0.15	4.1	99.2	.	.	.	.	.	.	.	18.0	92	26.9	58.1	11.9	6	2
	H_1		0.4	23.5	2.9	0.07	4.9	60.4	.	.	.	.	.	.	.	41.2	96	31.2	54.1	10.9	4	0
7	H_0	31	1.7	52.8	12.0	0.31	5.3	182.8	.	.	.	.	.	.	.	1.0	82	15.3	59.9	17.5	16	2
	H_1		2.1	48.0	8.9	0.35	5.3	182.8	.	.	.	.	.	.	.	17.2	82	17.7	63.3	14.6	18	0
8	H_0	30	1.7	43.5	8.7	0.24	4.3	106.3	11	2	9	0.02	<0.01	0.2	1.2	1.0	90	24.1	60.3	12.7	10	0
	H_1		0.8	26.5	3.3	0.09	4.8	53.4	.	.	.	.	.	.	.	28.3	94	28.7	60.5	7.6	6	0
9	H_0	34	0.8	40.0	5.3	0.18	4.9	86.3	.	.	.	.	.	.	.	1.0	92	20.9	60.7	14.4	8	0
	H_1		0.5	28.6	3.5	0.07	5.0	57.9	.	.	.	.	.	.	.	31.5	96	27.9	56.6	11.3	4	0
10	H_0	>50	0.9	39.5	4.0	0.18	4.3	161.5	.	.	.	.	.	.	.	12.0	90	24.6	58.9	12.7	8	2
	H_1		0.5	32.3	2.9	0.08	4.3	100.6	.	.	.	.	.	.	.	37.8	94	26.9	58.0	11.2	6	0
11	H_0	36	0.6	48.7	7.4	0.23	4.1	138.9	.	.	.	.	.	.	.	0.9	90	19.7	61.6	15.8	10	0
	H_1		0.4	25.3	2.4	0.06	4.1	81.7	.	.	.	.	.	.	.	17.5	96	25.6	55.0	15.4	4	0
12	H_0	31	0.6	50.5	6.5	0.19	4.9	126.3	11	4	7	0.02	0.04	0.4	2.8	0.7	92	22.1	59.4	15.3	6	2
	H_1		0.3	29.9	3.8	0.19	4.6	86.8	.	.	.	.	.	.	.	28.2	90	25.0	56.3	14.6	8	2
13	H_0	43	0.6	50.8	6.8	.	5.1	157.8	.	.	.	.	.	.	.	0.7	94	18.6	66.5	13.3	6	0
	H_1		0.4	30.8	3.6	.	4.6	81.7	.	.	.	.	.	.	.	26.7	90	31.4	54.9	11.3	8	2
14	H_0	>50	1.0	48.0	7.5	0.22	5.0	161.5	.	.	.	.	.	.	.	0.5	90	26.4	61.1	10.4	8	2
	H_1		0.5	30.1	2.8	0.07	4.6	73.1	.	.	.	.	.	.	.	15.4	94	29.9	56.3	10.5	4	2
15	H_0	"	1.5	58.0	11.8	0.31	4.9	173.6	18	7	11	0.05	0.01	0.8	5.6	0.3	96	35.0	55.5	7.5	4	0
	H_1		0.5	32.6	3.2	0.09	4.6	89.0	6	1	5	<0.01	0.01	0.1	1.0	19.1	96	37.2	53.6	6.2	4	0
16	H_0	"	0.8	51.7	9.0	0.26	4.9	161.5	.	.	.	.	.	.	.	0.9	94	30.1	59.7	8.1	4	2
	H_1		0.8	25.3	3.1	0.10	4.6	73.1	.	.	.	.	.	.	.	13.2	96	38.9	52.6	5.9	4	0
17	H_0	40	0.7	39.8	5.6	0.16	5.2	105.2	8	4	4	<0.01	<0.01	0.4	2.8	0.5	96	18.6	64.2	15.0	4	0
	H_1		0.5	33.2	2.6	0.06	4.6	66.1	5	1	4	<0.01	0.01	0.1	0.6	28.9	98	27.1	58.3	12.2	2	0
18	H_0	39	1.0	49.8	6.9	0.24	5.0	128.6	.	.	.	.	.	.	.	0.7	94	27.4	59.3	11.5	6	0
	H_1		0.7	28.5	4.4	0.12	4.6	95.1	.	.	.	.	.	.	.	25.3	94	25.6	56.6	14.3	6	0
19	H_0	36	0.9	44.6	6.6	0.22	5.4	141.7	12	6	6	0.01	0.01	0.9	4.4	0.6	90	13.5	67.3	16.9	8	2
	H_1		0.5	24.3	2.9	0.08	5.1	63.1	6	1	4	<0.01	0.01	0.1	1.0	36.6	94	27.9	54.5	14.1	6	0
20	H_0	34	6.9	98.7	41.2	1.00	4.8	257.2	62	25	37	0.07	0.05	1.8	24.0	20.7	80	36.3	41.6	14.6	10	10
	H_1		4.5	77.6	32.5	0.93	5.0	285.8	54	26	29	0.02	0.02	1.1	25.5	27.5	84	48.3	37.2	10.6	14	2
21	H_0	32	0.7	42.9	6.0	0.18	5.1	112.0	.	.	.	.	.	.	.	11.3	92	22.4	63.5	11.8	8	0
	H_1		0.5	22.4	3.2	0.08	5.0	63.1	.	.	.	.	.	.	.	25.0	96	25.1	59.9	11.1	2	2
22	H_0	35	0.9	36.0	5.1	0.15	4.7	119.7	.	.	.	.	.	.	.	0.8	92	20.6	62.5	14.9	6	2
	H_1		0.6	27.8	3.1	0.05	4.4	97.8	.	.	.	.	.	.	.	28.6	96	26.8	56.8	13.3	4	0
$\bar{x}$	H_0		1.3	49.6	8.8	0.27	4.9	148.7	19.3	8.2	11.1	0.04	0.03	0.84	6.7	12.5	90.4	29.0	55.2	12.4	8.1	1.6
	H_1		0.9	31.6	5.1	0.15	4.8	96.8	12.6	4.8	7.8	0.01	0.01	0.24	4.2	32.4	92.9	34.3	51.3	10.6	6.6	0.6
CV	H_0		100.0	25.4	87.5	66.7	8.2	26.6	80.3	82.9	90.1	75.0	66.7	58.3	101.5	144.8	4.5	40.0	19.0	25.8	38.3	131.3
	H_1		100.0	36.4	123.5	126.7	6.3	54.9	133.3	179.2	111.5	-	-	145.8	204.8	48.5	4.3	33.5	19.3	30.2	57.6	150.0

Table 4c. Soil analysis in the Recent ridge stands (cf. Table 4a).

			soil	water	chemical properties											texture (%)						
			H.M. (%)	W.H.C. (%)	O.M. (%)	Ntot (%)	pH	cond.	C.E.C.	T.E.B.	T.A.	K^+	Na^+	Mg^{2+}	Ca^{2+}	part.	sand	sand coarse	fract. med.	fine	silt	clay
									- - - - - - -		meq./100 g	- - - - - - - - - -										
1	H_0	7	3.6	84.9	23.0	0.86	4.4	201.3	25	8	18	0.6	1.80	1.5	4.6	87.8	84	35.4	39.9	20.0	14	2
	H_1		1.5	46.6	10.0	0.35	4.5	121.8	7	3	4	0.2	0.20	0.4	1.2	90.7	92	38.2	39.7	18.2	6	2
2	H_0	13	1.6	75.8	20.2	0.61	4.7	151.0	.	.	.	.	.	.	.	57.7	90	44.1	38.6	13.7	8	2
	H_1		0.7	31.1	6.5	0.17	4.9	82.7	.	.	.	.	.	.	.	78.5	96	57.7	32.6	6.2	4	0
3	H_0	10	1.5	52.3	13.2	0.39	4.1	173.6	15	5	11	0.2	0.20	0.5	2.6	76.4	90	29.2	43.3	23.4	8	2
	H_1		1.1	38.6	7.4	0.20	4.3	144.7	.	.	.	.	.	.	.	83.3	96	38.1	44.0	13.9	2	2
4	H_0	30	1.9	81.9	16.3	0.37	3.8	204.2	.	.	.	.	.	.	.	13.7	84	8.7	36.5	49.3	12	4
	H_1		0.5	37.6	4.2	0.10	3.9	151.0	.	.	.	.	.	.	.	25.0	90	8.5	43.6	41.8	8	2
5	H_0	24	1.2	45.1	7.7	0.26	5.3	113.8	7	5	2	0.1	0.02	0.6	3.2	27.9	98	20.9	69.6	7.1	2	0
	H_1		0.2	26.7	1.8	0.06	5.7	51.4	2	2	0	0.06	0.02	0.1	0.6	36.6	96	19.0	76.2	4.0	4	0
6	H_0	8	1.8	57.2	10.6	0.36	4.9	165.3	.	.	.	.	.	.	.	31.0	94	25.8	64.0	7.7	4	2
	H_1		0.9	36.0	3.4	0.11	4.9	99.2	.	.	.	.	.	.	.	69.3	98	9.2	65.7	3.8	2	0
7	H_0	9	1.7	75.7	23.0	0.74	4.1	210.4	29	7	22	0.4	0.09	1.3	5.2	78.8	90	22.8	61.0	13.2	10	0
	H_1		1.0	35.7	9.0	0.23	4.4	105.2	8	3	6	0.1	0.08	0.4	1.2	83.3	96	32.4	60.0	5.4	4	0
8	H_0	28	1.2	39.5	6.2	0.24	5.0	124.0	.	.	.	.	.	.	.	19.6	96	22.9	67.6	7.8	4	0
	H_1		0.4	29.7	2.0	0.08	5.3	72.3	.	.	.	.	.	.	.	26.8	98	21.5	71.3	6.2	2	0
9	H_0	26	1.0	46.4	5.7	0.21	5.2	106.8	.	.	.	.	.	.	.	23.9	96	31.6	59.4	7.2	2	2
	H_1		0.3	26.8	2.8	0.06	5.3	59.1	.	.	.	.	.	.	.	27.9	98	28.5	66.1	4.6	2	0
10	H_0	13	1.7	47.8	9.5	0.31	4.7	169.4	10	5	5	0.2	0.02	0.5	2.4	51.9	92	29.6	55.5	11.8	6	2
	H_1		0.5	31.0	4.0	0.14	5.1	89.0	4	2	2	0.08	0.02	0.3	1.0	54.8	98	34.6	55.8	8.2	2	0
11	H_0	5	3.6	97.0	24.7	0.85	5.1	154.3	28	15	14	0.4	0.07	1.7	11.6	57.4	88	14.5	64.5	16.2	10	2
	H_1		0.6	24.0	3.1	0.11	5.5	75.5	4	3	1	0.06	0.03	0.3	1.4	77.9	98	26.8	66.5	4.5	2	0
12	H_0	7	2.4	70.9	16.5	0.54	5.1	182.7	.	.	.	.	.	.	.	58.4	92	17.9	69.3	9.6	6	2
	H_1		0.5	34.5	3.7	0.10	5.2	77.2	.	.	.	.	.	.	.	60.5	98	27.1	68.4	3.1	2	0
13	H_0	10	1.0	78.3	18.0	0.53	4.7	157.8	.	.	.	.	.	.	.	43.4	92	16.0	68.3	11.4	6	2
	H_1		0.6	29.4	3.0	0.09	5.1	56.7	.	.	.	.	.	.	.	61.3	98	28.1	63.3	5.2	2	0
14	H_0	5	0.7	51.1	9.0	0.28	5.1	121.8	12	5	7	0.1	0.05	0.4	3.0	19.7	94	19.9	69.5	8.0	6	0
	H_1		0.2	30.2	2.5	0.09	5.4	52.4	3	2	1	0.09	0.07	0.1	0.4	78.0	98	26.8	66.1	4.8	2	0
15	H_0	6	3.1	91.5	26.0	1.01	4.5	165.3	.	.	.	.	.	.	.	87.9	90	24.2	52.4	17.4	8	2
	H_1		0.6	27.5	5.4	0.13	5.0	66.1	.	.	.	.	.	.	.	94.4	98	35.4	58.7	4.1	2	0
16	H_0	12	3.9	102.9	29.9	0.79	4.5	192.9	.	.	.	.	.	.	.	76.5	92	23.8	55.0	16.8	8	0
	H_1		0.4	30.7	4.7	0.14	4.9	79.8	.	.	.	.	.	.	.	81.4	96	38.0	55.5	4.6	4	0
17	H_0	16	5.6	83.0	27.7	0.90	6.2	560.0	35	35	0.2	0.04	0.20	1.4	30.3	51.0	64	27.1	34.9	18.9	32	4
	H_1		1.4	47.1	7.9	0.33	6.2	439.5	13	13	0	0.1	0.10	0.5	11.4	73.2	92	35.7	49.7	8.8	8	0
18	H_0	15	1.3	62.5	14.3	0.33	4.0	182.7	18	3	15	0.2	0.10	0.5	1.2	68.5	90	46.7	40.7	8.9	8	2
	H_1		0.6	23.5	3.3	0.09	4.3	75.5	4	2	2	0.06	0.07	0.1	0.2	69.5	96	62.3	31.5	4.6	2	2
19	H_0	6	3.1	99.6	26.1	0.79	4.5	131.0	.	.	.	.	.	.	.	51.0	76	32.0	43.5	18.9	20	4
	H_1		1.5	37.6	8.7	0.29	4.6	84.7	.	.	.	.	.	.	.	74.2	92	42.7	33.9	14.9	8	0
20	H_0	8	2.2	69.3	17.3	0.56	4.5	138.9	.	.	.	.	.	.	.	64.6	88	40.0	43.9	12.9	12	0
	H_1		1.1	49.0	9.6	0.30	4.6	126.3	.	.	.	.	.	.	.	80.7	92	47.6	36.4	12.0	8	0
21	H_0	8	2.6	74.6	17.3	0.57	5.1	121.8	.	.	.	.	.	.	.	49.6	82	20.8	42.5	26.3	16	2
	H_1		1.3	38.5	7.6	0.23	4.8	84.7	.	.	.	.	.	.	.	93.5	92	35.5	42.1	14.4	2	0
$\bar{x}$	H_0		2.2	70.8	17.3	0.58	4.7	177.9	19.9	9.8	10.5	0.25	0.28	0.93	7.1	52.2	88.7	26.4	53.3	15.5	9.6	1.7
	H_1		0.8	33.9	5.3	0.16	5.0	104.5	5.6	3.8	2.0	0.09	0.07	0.28	2.2	67.7	95.6	33.0	53.7	9.1	3.7	0.4
CV	H_0		54.6	27.0	42.8	43.1	10.6	52.3	48.7	103.1	70.5	72.0	203.5	57.0	129.6	43.9	8.6	36.4	23.5	61.3	70.8	76.5
	H_1		50.0	21.5	50.9	56.3	10.0	78.3	64.3	100.0	105.0	55.6	85.7	57.1	172.7	32.2	2.8	40.3	26.3	95.6	64.9	200.0

Table 5. Variations in soil characters between the horizons H_0 and H_1 (Ancylus, Litorina, Recent ridge). The figures are means of values from all stands of each ridge. Values under "t" have one asterisk for significant variations (at a 5 % probability level) and two for highly significant variations (at a 1 % probability level).

horizon		H_0	H_1	t
soil water:				
H.M. (%)	A	1.2	0.6	7.23**
	L	1.3	0.9	1.19
	R	2.2	0.8	4.98**
W.H.C. (%)	A	47.26	29.15	6.81**
	L	49.60	31.55	4.99**
	R	70.82	33.90	8.26**
chemical properties:				
O.M. (%)	A	7.76	3.51	0.72
	L	8.84	5.12	1.76
	R	17.28	5.27	6.98**
Ntot (%)	A	0.24	0.11	6.19**
	L	0.27	0.15	2.09*
	R	0.58	0.16	7.24**
pH	A	5.4	5.3	0.95
	L	4.9	4.8	0.93
	R	4.7	5.0	-1.81
cond. (µmhos/cm)	A	206.3	92.2	6.45**
	L	148.7	96.8	3.68**
	R	177.6	104.5	2.71**
C.E.C. (meq./100 g)	A	12.48	7.41	2.59*
	L	19.33	12.63	0.83
	R	19.89	5.63	3.91**
T.E.B.	A	5.6	1.7	3.36**
	L	8.2	4.75	0.97
	R	9.78	3.75	1.59
T.A.	A	6.88	5.71	0.89
	L	11.11	7.75	0.74
	R	10.47	2.00	3.11**
K^+	A	0.24	0.12	2.99**
	L	0.042	0.011	2.85*
	R	0.025	0.094	2.36*
chemical properties:				
Na^+	A	0.046	0.045	0.06
	L	0.028	0.011	2.77*
	R	0.283	0.074	0.53
Mg^{2+}	A	0.83	0.24	2.69*
	L	0.84	0.24	2.86**
	R	0.93	0.28	3.35**
Ca^{2+}	A	4.63	1.29	3.43**
	L	6.73	4.24	0.67
	R	7.12	2.18	1.41
texture (%):				
particles (>2 mm)	A	2.51	5.98	-2.45*
	L	12.51	32.36	-1.93
	R	52.22	67.66	-2.24*
sand	A	93.1	94.9	-2.78**
	L	90.4	92.9	-1.73
	R	88.7	95.6	-3.91**
coarse	A	18.73	21.82	-1.39
	L	29.01	34.26	-1.36
	R	26.38	33.03	-1.86
medium	A	56.99	52.83	3.61**
	L	55.19	51.27	1.27
	R	53.33	53.67	0.083
fine	A	21.26	22.28	-0.488
	L	12.39	10.55	1.93
	R	15.54	9.11	2.28*
silt	A	4.9	3.9	2.37*
	L	8.1	6.6	1.44
	R	9.6	3.7	3.75**
clay	A	2.1	1.1	2.65*
	L	1.6	0.6	2.02*
	R	1.7	0.4	3.88**

Table 6. Variations in soil characters between the Ancylus, Litorina, and Recent ridge within the horizons H_0 and H_1. The figures are means of values from all stands of each ridge. Values under "F" have one asterisk for significant variations (at a 5 % probability level) and two for highly significant variations (at a 1 % probability level). The same letter (a or b) under two or three mean values indicates that they are significantly different according to LSD test.

horizon	H_0				H_1			
ridge	A	L	R	F	A	L	R	F
soil water:								
H.M. (%)	1.2 a	1.3 b	2.2 a b	7.44**	0.6 a	0.9 a	0.8	1.07
W.H.C. (%)	46.26 a	49.60 b	70.82 a b	17.88**	29.15	31.55	33.90	1.89
chemical properties:								
O.M. (%)	7.76 a	8.84 b	17.28 a b	16.00**	3.51	5.12	5.27	1.53
N tot (%)	0.24 a	0.27 b	0.58 a b	21.45**	0.11	0.15	0.16	1.33
pH	5.4 a b	4.9 a	4.7 b	13.29**	5.3 a	4.8 a	5.0 a	10.00**
cond. (µmhos/cm)	206.3 a	148.7 a	177.6	3.47*	92.2	96.8	104.5	0.27
C.E.C. (meq./100 g)	12.48	19.33	19.89	1.88	7.41	12.63	5.63	1.33
T.E.B.	5.6	8.2	9.78	1.15	1.7	4.75	3.75	1.18
T.A.	6.88	11.11	10.47	1.37	5.71	7.75 a	2.0 a	2.75
K^+	0.24 a	0.042 a b	0.25 b	6.80**	0.12 a	0.011 a b	0.094 b	16.67**
Na^+	0.046	0.028	0.283	2.33	0.045	0.011 a	0.074 a	3.54*
Mg^{+2}	0.83	0.84	0.93	0.08	0.24	0.24	0.28	0.09
Ca^{+2}	4.63	6.73	7.12	0.57	1.29	4.24	2.18	1.02
texture (%):								
particles (>2 mm)	2.51 a	12.51 a	52.22 a	61.55**	5.98 a	32.36 a	67.66 a	20.71**
sand	93.1 a	90.4	88.7 a	5.17**	94.9 a	92.9 a b	95.6 b	4.66*
coarse	18.73 a b	29.01 a	26.38 b	8.04**	21.82 a b	34.26 a	33.03 b	9.97**
medium	56.99	55.19	53.33	0.95	52.83	51.27	53.67	0.34
fine	21.26 a b	12.39 a	15.54 b	11.31**	22.28 a b	10.55 a	9.11 b	22.38**
silt	4.9 a b	8.1 a	9.6 b	8.87**	3.9 a	6.6 a b	3.7 b	7.98**
clay	2.1	1.6	1.7	0.63	1.1 a	0.6	0.4 a	4.15*

Table 7. Local climatic data recorded during four weeks (July–August 1977), in an open meadow, in a glade, and in closed forest (Ancylus, Litorina, Recent ridge). Left: weekly values obtained from an instrument located in the same place (Litorina ridge) during all four weeks; right: weekly values obtained simultaneously from an instrument located in different places each week. Fluctuations of minimum, maximum, and mean values for temperature (T) and relative humidity (RH) are expressed by standard deviations (SD).

week no.		1		2		3		4	
precipitation (mm)		4.1		40.9		1.3		12.6	
ridge		L	A	L	L	L	R	L	L
habitat		open	open	open	glade	open	open	open	forest
RH (%)	min.	61.3	60.0	67.8	66.4	55.3	56.5	56.5	58.8
	max.	95.0	95.3	94.8	95.3	96.2	97.5	95.2	97.2
	mean	79.8	79.0	83.7	83.5	79.8	79.5	77.5	78.8
T (°C)	min.	10.0	10.1	12.5	12.2	10.1	11.1	11.0	11.3
	max.	17.3	17.1	17.8	17.9	20.9	20.5	20.8	19.3
	mean	13.8	13.8	14.8	14.8	16.0	16.3	16.2	15.7
WV (m/sec.)	min.	1.2	2.4	1.2	0.6	1.1	1.9	0.9	0.4
	max.	2.8	4.4	2.8	1.6	2.6	4.2	2.3	1.2
SD									
RH	min.	13.9	10.5	11.4	12.1	8.4	6.6	19.6	18.8
	max.	4.4	4.6	3.1	4.1	1.2	1.4	2.7	2.6
	mean	13.7	13.3	10.9	11.5	15.7	15.2	18.9	18.7
T	min.	3.8	3.4	0.6	0.7	1.5	1.6	2.7	2.3
	max.	1.6	1.9	1.6	1.7	1.5	0.8	1.3	1.3
	mean	2.9	2.8	1.9	2.0	3.8	3.1	3.7	2.9

Table 8. Distribution of common field layer species along gradients (5 categories) of relative light and vegetation moisture index, expressed by mean cover values. Closed forest stands are in the category 1 of relative light and open meadow stands in category 5; stands in category 1 of the vegetation moisture index are very dry and those in category 5 are wet (cf. "Distribution of species in relation to light and moisture").

	relative light					moisture index				
categories	1	2	3	4	5	1	2	3	4	5
Veronica spicata	.	.	0.03	0.2	3.7	6.1	2.7	0.1	.	.
Thymus serpyllum	.	.	0.01	0.2	6.6	14.3	2.8	0.2	.	.
Hieracium pilosella	.	0.1	0.4	1.5	4.5	5.9	3.1	1.3	0.1	.
Sedum acre	.	.	.	0.1	3.4	5.9	2.3	0.03	.	.
Artemisia campestris	.	.	.	.	0.8	1.7	0.2	.	.	.
Saxifraga granulata	.	0.03	.	0.1	0.9	1.2	0.7	0.03	0.01	.
Helianthemum nummularium	.	.	0.2	0.7	3.6	5.3	3.5	0.1	.	.
Potentilla tabernaemontani	.	.	0.2	0.3	3.2	6.1	1.9	1.0	0.01	.
Festuca ovina	.	0.7	4.1	3.1	16.3	24.9	10.7	4.1	0.8	.
Arrhenatherum pratense	.	0.04	0.2	3.4	5.0	5.7	5.7	1.4	0.02	.
Campanula rotundifolia	0.1	0.4	1.1	2.3	2.5	4.2	1.5	1.2	0.2	.
Carex caryophyllea	.	.	0.02	0.4	0.7	0.6	0.9	0.3	.	.
Galium verum	0.04	1.2	3.3	9.6	10.8	10.9	11.9	6.1	0.3	.
Calluna vulgaris	0.1	0.3	4.2	15.1	7.0	0.4	15.1	4.5	2.2	.
Veronica chamaedrys	1.6	3.9	5.4	8.0	2.3	0.5	2.6	7.0	1.5	0.2
Poa angustifolia	0.1	3.5	6.9	10.0	6.1	1.7	10.6	7.6	0.6	.
Arrhenatherum pubescens	0.1	0.7	0.3	9.0	1.0	0.1	1.5	3.5	0.1	1.8
Achillea millefolium	0.01	0.2	2.1	6.0	6.5	7.1	5.7	3.8	0.1	.
Agrostis tenuis	1.4	6.9	10.7	5.2	5.2	6.1	3.2	8.7	2.1	.
Anemone pratensis	.	0.1	1.9	2.4	2.1	4.2	0.9	1.0	0.3	.
Anthoxanthum odoratum	0.2	3.4	4.8	1.0	0.3	0.9	1.1	1.2	2.8	.
Phleum phleoides	.	0.8	1.3	2.6	5.1	6.0	5.5	2.0	0.4	.
Anthriscus sylvestris	0.7	5.2	1.1	2.0	0.02	0.03	0.03	2.4	1.7	.
Deschampsia flexuosa	7.3	6.9	9.4	5.0	4.0	0.1	6.4	6.5	7.3	.
Hypericum perforatum	0.2	0.6	1.1	0.8	0.9	0.8	1.6	0.9	0.2	0.2
Knautia arvensis	0.01	1.3	2.1	1.4	0.5	0.2	0.4	1.5	0.7	.
Luzula campestris	.	0.2	0.9	2.0	2.8	2.9	2.8	1.2	0.3	.
Plantago lanceolata	.	0.04	1.5	3.3	4.3	5.2	3.6	2.2	0.01	.
Ranunculus bulbosus	.	.	0.2	0.3	0.9	1.6	0.5	0.3	.	.
Rumex acetosella	.	.	0.2	0.1	2.3	4.3	2.1	0.2	0.03	.
Silene nutans	.	0.3	0.3	0.04	1.6	2.7	1.0	0.1	0..	.
Viscaria vulgaris	.	0.1	0.2	0.3	2.4	1.3	4.1	0.2	0.1	.
Fragaria vesca	0.8	0.5	1.3	5.5	0.1	0.1	.	2.4	0.5	2.
Allium vineale	0.04	0.5	0.4	0.9	1.2	1.0	1.7	0.6	0.3	4.0
Festuca rubra	0.4	2.5	2.7	1.5	1.4	1.9	1.4	2.5	0.8	.
Arrhenatherum elatius	.	5.4	7.1	5.7	0.1	.	0.1	5.4	1.8	4.2
Dactylis glomerata	1.1	2.7	5.9	2.6	0.6	0.03	1.2	3.1	1.8	0.9
Rumex acetosa	0.3	1.0	1.8	0.5	0.7	0.1	0.2	1.3	0.2	.
Laserpitium latifolium	0.3	0.4	0.6	2.4	0.1	.	0.1	0.9	0.4	0.2
Veronica officinalis	0.3	0.3	0.6	0.1	0.1	.	0.1	0.3	0.4	.
Viola riviniana	4.9	1.4	0.7	0.5	0.2	.	0.3	0.9	3.4	2.3
Anemone nemorosa	14.4	3.3	0.8	1.5	0.2	.	0.2	1.5	9.1	10.2
Hepatica nobilis	10.9	3.2	0.4	0.3	0.1	0.03	.	1.1	9.6	.
Melampyrum pratense	6.4	5.2	4.2	4.7	0.5	0.4	1.1	4.4	5.4	0.2
Melica nutans	0.9	3.0	3.4	3.4	0.1	.	0.1	3.1	1.5	.
Stellaria holostea	5.5	6.1	3.1	1.6	0.01	.	0.02	3.2	6.7	.
Mercurialis perennis	7.3	1.2	1.4	0.7	0.1	0.03	.	1.3	4.6	.
Convallaria majalis	17.8	3.7	6.9	0.1	0.01	.	0.02	3.4	12.7	.
Lathyrus montanus	1.1	0.7	0.6	0.2	0.02	.	0.02	0.7	0.7	.
Luzula pilosa	1.8	0.9	0.9	0.1	.	.	.	0.4	1.7	.
Oxalis acetosella	5.7	0.02	0.01	.	.	.	.	0.03	3.8	.
Maianthemum bifolium	5.6	0.3	.	0.03	.	0.01	.	0.01	4.0	.
Poa nemoralis	0.9	6.0	1.4	0.2	.	.	.	0.6	4.6	0.3
Primula veris	1.0	0.2	0.7	0.1	0.2	0.1	0.3	0.3	0.7	0.5
Geum urbanum	1.5	0.4	0.7	0.5	0.01	0.03	.	0.5	1.1	.
Dentaria bulbifera	3.3	0.02	.	0.04	.	.	.	0.02	2.2	.

Table 9a. Environmental data and mean occurrence values for common species in the Ancylus ridge vegetation groups (subgroups), obtained by application of agglomerative classification (cf. Figs. 5 a-c). Environmental data are given as mean values for the stands of each group (subgroup); soil property values are given for both soil horizons (H_0 and H_1), only when there are significant differences between them (cf. Table 5).

VEGETATIONAL GROUP – SUBGROUP		A		B		C		A_2		A_1		C_2		C_1	
moisture index		1-2		3		3-4		1		2		3-4		4	
mean relative light	(%)	94.2		59.6		27.3		93.4		95.0		38.3		16.3	
mean tree-shrub cover sum	(%)	1.5		11.9		100.8		0.12		2.3		67.7		133.9	
mean litter cover sum	(%)	11.3		50.6		84.4		10.0		12.5		67.5		101.3	
horizon		H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1
soil water	H.M. (%)	1.05	0.57	1.08	0.63	1.52	0.77	1.06	0.58	1.03	0.55	1.13	0.54	1.90	1.00
water	W.H.C. (%)	41.6	27.2	46.7	30.0	55.6	32.0	43.5	26.7	39.7	27.6	44.2	26.5	66.9	37.5
	O.M. (%)	5.5	–	7.1	–	10.3	–	6.3	–	4.7	–	6.5	–	15.0	–
	N_{tot} (%)	0.23	0.11	0.24	0.12	0.29	0.15	0.27	0.10	0.18	0.11	0.17	0.07	0.40	0.22
	pH	5.6	–	5.7	–	5.0	–	5.5	–	5.6	–	5.0	–	5.0	–
chemical	cond. (µmhos/cm)	149.2	67.6	234.3	93.9	243.2	119.7	173.0	78.0	125.4	57.1	192.0	82.8	294.4	156.5
properties	C.E.C.(meq./100 g)	9.4	7.0	10.9	6.2	18.8	10.9	10.6	7.4	8.1	6.5	10.5	5.5	27.0	16.2
	T.E.B.	4.6	1.5	5.7	2.1	8.9	2.3	6.05	1.6	3.2	1.3	3.4	0.94	14.4	3.6
	T.A.	4.8	–	5.9	–	9.9	–	4.6	–	4.9	–	7.1	–	12.7	–
	K^+	0.23	0.10	0.25	0.13	0.30	0.15	0.29	0.10	0.17	0.10	0.10	0.10	0.50	0.20
	Na^+	0.03	–	0.03	–	0.10	–	0.03	–	0.03	–	0.04	–	0.15	–
	Mg^{2+}	0.65	0.16	0.80	0.30	1.50	0.35	0.80	0.20	0.50	0.12	0.40	0.10	2.60	0.60
	Ca^{2+}	3.7	1.1	4.7	1.5	7.5	1.8	4.8	1.2	2.6	0.9	2.9	0.75	12.0	2.8
	particles (>2 mm)	5.1	8.7	1.3	4.7	1.2	6.4	8.2	12.1	1.9	5.2	1.5	4.9	0.9	7.9
	sand	93.8	96.5	93.6	95.2	91.0	92.9	93.6	96.0	94.0	97.0	94.0	95.3	88.0	90.5
	coarse	23.2	–	15.0	–	19.6	–	25.9	–	20.4	–	14.8	–	24.4	–
texture (%)	medium	55.7	53.8	59.6	54.9	56.6	51.5	53.8	51.1	57.5	56.4	55.4	49.2	57.7	53.7
	fine	17.6	–	22.5	–	21.2	–	16.4	–	18.8	–	27.3	–	15.1	–
	silt	4.4	3.0	4.7	3.7	5.8	5.2	4.8	3.5	4.0	2.5	4.5	3.8	7.0	6.5
	clay	1.8	0.5	1.7	1.1	3.3	2.0	1.6	0.5	2.0	0.5	1.5	0.9	5.0	3.0
tree-shrub layer (mean cover):															
Corylus avellana		0.05		0.5		20.3		0.1		.		1.6		40.0	
Quercus robur		.		0.3		11.5		.		.		1.7		21.3	
Betula verrucosa		0.02		.		10.0		0.04		.		.		20.0	
Sorbus aucuparia		.		.		10.7		.		.		10.0		11.3	
Ribes alpinum		.		.		2.3		.		.		1.9		2.6	
Pinus sylvestris		.		.		22.9		.		.		45.8		.	
Fraxinus excelsior		.		.		2.2		.		.		4.3		0.1	
Acer platanoides		.		.		0.6		.		.		1.2		.	
Prunus spinosa		.		10.5		2.1		.		.		0.5		3.6	
Juniperus communis		.		0.2		0.7		.		2.8		.		1.3	
field layer (mean frequency):															
Galium verum		95.0		58.0		8.8		94.4		95.5		17.5		.	
Veronica spicata		46.4		2.1		.		76.8		16.0		.		.	
Festuca ovina		54.6		5.8		5.7		69.6		39.5		11.3		.	
Campanula rotundifolia		36.4		11.1		2.2		63.2		9.5		4.3		.	
Potentilla tabernaemontani		41.7		3.1		.		60.8		22.5		.		.	
Thymus serpyllum		29.9		0.2		.		55.2		4.5		.		.	
Hieracium pilosella		35.7		2.4		.		52.8		18.5		.		.	
Sedum acre		40.5		0.7		.		52.0		29.0		.		.	
Achillea millefolium		40.6		35.8		2.9		49.2		32.0		5.3		0.5	
Anemone pratensis		28.5		10.2		0.8		46.4		10.5		1.5		.	
Stellaria graminea		25.6		3.1		0.2		43.2		8.0		0.3		.	
Luzula campestris		30.6		7.8		1.2		43.2		18.0		2.3		.	
Plantago lanceolata		34.9		21.6		0.3		36.8		33.0		0.5		.	
Artemisia campestris		18.2		.		.		30.4		6.0		.		.	
Saxifraga granulata		20.0		.		.		28.0		12.0		.		.	
Helianthemum nummularium		16.3		1.8		.		28.0		4.5		.		.	
Silene nutans		18.6		0.7		1.4		27.6		9.5		2.8		.	
Hypericum perforatum		16.3		16.9		3.4		25.6		7.0		4.3		2.5	
Ranunculus bulbosus		12.0		5.3		.		18.4		5.5		.		.	
Rumex acetosella		7.0		0.7		0.3		10.0		4.0		0.5		.	
Arrhenatherum pratense		69.6		17.8		0.9		61.2		78.0		1.8		.	
Phleum phleoides		70.8		26.4		9.5		63.6		78.0		19.0		.	
Calluna vulgaris		22.3		.		.		3.6		41.0		.		.	
Veronica chamaedrys		26.8		68.9		19.7		9.6		44.0		17.8		21.5	
Agrostis tenuis		24.6		66.2		16.7		39.2		10.0		33.3		.	
Poa angustifolia		44.2		64.4		12.3		28.4		60.0		23.5		1.0	
Prunus spinosa		4.0		36.7		3.4		6.0		2.0		1.8		5.0	
Arrhenatherum pubescens		2.7		35.1		0.7		0.8		4.5		0.3		1.0	
Fragaria vesca		2.2		33.1		8.0		4.4		.		0.5		15.5	
Dactylis glomerata		0.4		28.2		20.9		0.8		.		25.3		16.5	
Festuca rubra		2.0		21.8		8.2		0.4		3.5		11.3		5.0	
Anthriscus sylvestris		0.7		20.9		4.5		0.4		1.0		8.5		0.5	
Knautia arvensis		2.4		18.9		9.2		3.2		1.5		16.3		2.0	
Roegneria canina		0.2		18.2		5.9		0.4		.		11.8		.	
Rumex acetosa		0.8		17.3		7.8		1.6		.		10.0		5.5	
Allium vineale		3.0		9.1		1.9		2.0		4.0		2.8		1.0	
Primula veris		0.6		9.0		5.2		1.2		.		10.0		0.3	
Anthoxanthum odoratum		13.7		5.1		26.9		20.4		7.0		50.8		3.0	
Arrhenatherum elatius		.		2.2		19.8		.		.		39.5		.	
Poa nemoralis		.		4.2		14.4		.		.		20.8		8.0	
Rubus caesius		.		0.2		11.7		.		.		17.8		5.5	
Sorbus aucuparia		0.2		1.1		10.3		0.4		.		15.5		5.0	
Melica nutans		.		0.4		6.5		.		.		12.0		1.0	
Hepatica nobilis		0.2		5.3		46.5		0.4		.		7.0		86.0	
Melampyrum pratense		2.0		42.9		35.3		4.0		.		1.0		69.5	
Convallaria majalis		.		2.2		35.2		.		.		13.0		57.3	
Viola riviniana		0.8		9.3		30.8		.		1.5		8.5		53.0	
Fraxinus excelsior		0.4		7.6		37.8		0.8		.		25.3		50.0	
Oxalis acetosella		.		0.2		20.5		.		.		0.5		40.5	
Stellaria holostea		.		12.7		33.3		.		.		31.5		35.0	
Geum urbanum		0.6		12.4		16.5		1.2		.		1.5		31.5	
Maianthemum bifolium		0.2		.		14.4		0.4		.		1.3		27.5	
Luzula pilosa		.		.		14.8		.		.		6.5		23.0	
Deschampsia flexuosa		1.2		3.0		14.9		0.8		1.5		9.3		20.5	
Mercurialis perennis		1.0		7.3		9.7		2.0		.		0.8		18.5	
Quercus robur		.		3.3		10.5		.		.		9.0		12.0	
Lasierpitium latifolium		.		2.2		5.9		.		.		1.3		10.0	
Veronica officinalis		.		0.4		7.5		.		.		7.0		8.0	
Corylus avellana		.		0.9		5.2		.		.		2.3		8.0	
Serratula tinctoria		.		3.3		4.0		.		.		.		8.0	
Polygonatum multiflorum		0.2		0.2		3.9		0.4		.		3.3		4.5	
Rosa spp.		0.5		0.7		2.7		0.4		0.5		1.3		4.0	
bottom layer (mean presence):															
Abietinella abietina		62.5		11.0		.		100.0		25.0		.		.	
Rhytidiadelphus squarrosus		62.5		44.0		6.5		100.0		25.0		13.0		.	
Hypnum cupressiforme		32.5		22.0		19.0		40.0		25.0		13.0		25.0	
Brachythecium albicans		57.5		33.0		6.5		40.0		75.0		13.0		.	
Rhodobryum roseum		35.0		33.0		19.0		20.0		50.0		13.0		25.0	
Mnium affine		80.0		100.0		25.0		60.0		100.0		.		50.0	
Brachythecium velutinum		.		44.0		12.5		.		.		.		25.0	
Cirriphyllum piliferum		.		44.0		12.5		.		.		.		25.0	
Pleurozium schreberi		37.5		11.0		37.5		.		75.0		75.0		.	
Brachythecium rutabulum		22.0		55.0		62.5		20.0		25.0		50.0		75.0	

Table 9b. Environmental data and mean occurrence values in the Litorina ridge vegetation groups (subgroups) (cf. Table 9a).

VEGETATIONAL GROUP - SUBGROUP		K_1		K_2		L		M		L_0		L_1		M_0		M_2	
moisture index		2		2-5		3-4		4		3		3-4		4		4	
mean relative light	(%)	100.0		64.0		40.1		12.9		45.3		34.8		12.0		13.7	
mean tree-shrub cover sum	(%)	.		21.3		63.9		126.1		57.9		69.9		116.6		135.5	
mean litter cover sum	(%)	20.0		36.7		70.7		106.7		67.5		73.8		115.0		98.3	
horizon		H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1
Soil water	H.M. (%)	1.20	-	1.22	-	0.89	-	1.7	-	0.70	-	1.08	-	2.5	-	0.90	-
	W.H.C. (%)	54.1	27.3	43.7	30.4	45.2	29.4	56.3	34.3	45.4	27.5	45.0	31.3	63.9	42.8	26.0	
chemical properties	O.M. (%)	9.6	-	8.3	-	6.6	-	12.2	-	6.0	-	7.2	-	16.8	-	7.5	-
	N_{tot} (%)	0.41	0.08	0.24	0.15	0.21	0.10	0.38	0.23	0.20	0.10	0.21	0.09	0.51	0.36	0.24	0.10
	pH	4.9	-	4.9	-	4.8	-	5.1	-	4.6	-	5.0	-	5.0	-	5.1	-
	cond. (µmhos/cm)	169.4	69.4	133.3	100.2	140.1	87.4	165.7	104.8	134.7	83.1	145.5	91.7	187.5	132.4	143.9	77..
	C.E.D.(meq./100 g)	22.0	-	11.0	-	11.3	-	31.0	-	11.0	-	11.5	-	40.0	-	12.0	-
	T.E.B.	11.0	-	2.0	-	4.3	-	11.0	-	4.0	-	5.5	-	16.0	-	6.0	-
	T.A.	11.0	-	9.0	-	6.5	-	15.0	-	7.0	-	6.0	-	24.0	-	6.0	-
	K^+	0.10	<0.01	0.02	.	0.03	<0.01	0.04	0.01	0.02	<0.01	0.03	<0.01	0.06	0.01	0.01	<0.01
	Na^+	0.04	<0.01	<0.01	-	0.03	<0.01	0.02	0.20	0.04	<0.01	0.02	<0.01	0.03	0.02	0.01	0.01
	Mg^{2+}	1.30	-	0.20	-	0.53	-	1.10	-	0.40	-	0.65	-	1.30	-	0.90	-
	Ca^{2+}	8.8	0.10	1.2	-	3.4	0.13	9.6	0.35	2.8	0.10	3.9	0.15	14.8	0.60	4.4	0.10
textures (%)	particles (>2 mm)	24.4	-	17.9	-	14.9	-	3.2	-	6.2	-	23.5	-	5.6	-	0.7	-
	sand	84.0	-	89.7	-	91.0	-	91.3	-	91.0	-	91.0	-	90.0	-	92.7	-
	coarse	45.9	-	31.4	-	27.1	-	26.4	-	22.2	-	31.9	-	29.1	-	23.7	-
	medium	34.7	-	52.6	-	54.4	-	59.2	-	60.9	-	47.9	-	56.2	-	62.1	-
	fine	14.0	-	11.8	-	13.2	-	11.3	-	13.9	-	12.4	-	11.5	-	12.2	-
	silt	14.0	-	9.0	-	7.5	-	6.5	-	8.0	-	7.0	-	7.0	-	6.0	-
	clay	2.0	2.0	1.3	.	1.0	0.5	2.2	0.3	1.0	1.0	1.0	.	3.0	1.5	1.3	.
tree-shrub layer (mean cover):																	
Corylus avellana		.		1.9		5.7		57.4		0.2		11.1		54.1		60.6	
Quercus robur		.		2.8		46.7		43.2		54.4		38.7		26.3		60.1	
Betula verrucosa		.		11.5		10.7		13.7		1.8		19.5		22.1		5.3	
Sorbus aucuparia		.		.		0.2		2.5		0.1		0.2		0.8		4.2	
Juniperus communis		.		1.9		0.3		0.4		0.6		.		0.7		.	
Ribes alpinus		.		.		0.1		0.4		0.1		.		0.4		0.4	
Crataegus spp.		.		.		.		0.4		.		.		0.2		0.5	
Fraxinus excelsior		.		2.0		0.1		2.0		.		0.1		3.7		0.2	
Lonicera xylosteum		.		0.1		0.2		0.2		0.2		0.1		0.4		.	
field layer (mean frequency):																	
Allium vineale		97.0		10.0		6.7		3.4		.		13.3		.		6.7	
Helianthemum nummularium		93.0		11.2		.		.		.		.		.		.	
Galium verum		80.0		30.5		15.8		0.4		31.5		.		0.8		.	
Plantago lanceolata		77.0		12.8		0.4		.		0.8		.		.		.	
Luzula campestris		70.0		26.8		4.3		.		8.5		.		.		.	
Saxifraga granulata		70.0		7.8		0.9		.		.		1.8		.		.	
Festuca ovina		43.0		17.2		3.4		.		6.8		.		.		.	
Festuca rubra		40.0		4.3		0.8		.		1.5		.		.		.	
Arrhenatherum pratense		27.0		14.5		.		.		.		.		.		.	
Anemone pratensis		20.0		6.2		1.3		.		2.5		.		.		.	
Rosa spp.		7.0		2.1		1.7		1.7		2.5		0.8		3.3		.	
Achillea millefolium		50.0		52.2		9.2		.		18.3		.		.		.	
Poa angustifolia		40.0		46.2		25.4		.		40.0		10.8		.		.	
Calluna vulgaris		.		37.8		.		.		.		.		.		.	
Campanula rotundifolia		13.0		24.3		4.2		0.4		6.5		1.8		0.8		.	
Arrhenatherum elatius		.		24.1		3.8		.		.		7.5		.		.	
Campanula persicifolia		.		21.0		7.6		.		4.3		10.8		.		.	
Dactylis glomerata		.		20.5		6.7		0.4		.		13.3		0.8		.	
Arrhenatherum pubescens		3.0		15.0		2.9		0.4		2.5		3.3		0.8		.	
Anthoxanthum odoratum		.		12.7		11.8		.		11.8		11.8		.		.	
Knautia arvensis		.		11.0		4.5		.		6.5		2.5		.		.	
Rumex acetosa		.		10.5		7.3		1.6		4.0		10.0		0.8		2.3	
Deschampsia flexuosa		.		50.0		60.0		7.4		82.5		37.5		9.0		5.7	
Veronica chamaedrys		.		17.7		54.2		21.3		62.5		45.3		19.3		23.3	
Agrostis tenuis		.		8.3		39.7		.		60.0		19.3		.		.	
Trifolium medium		.		11.0		24.6		.		38.3		10.8		.		.	
Lathyrus montanus		.		1.1		24.7		11.1		27.5		21.8		12.5		9.7	
Hypericum perforatum		.		12.0		9.7		1.3		17.5		1.8		2.5		.	
Prunus spinosa		.		1.1		5.1		0.4		8.3		1.8		0.8		.	
Melampyrum pratense		.		41.0		85.9		43.0		81.8		90.0		19.3		66.7	
Stellaria holostea		.		.		70.3		66.2		56.8		83.8		63.3		69.0	
Melica nutans		.		4.5		61.1		8.0		54.3		67.8		7.3		8.7	
Aegopodium podagraria		.		17.8		24.2		0.4		.		48.3		0.8		.	
Anthriscus sylvestris		.		1.2		16.3		1.2		.		32.5		.		2.3	
Laserpitium latifolium		.		5.5		14.2		0.9		.		28.3		1.8		.	
Luzula pilosa		.		.		17.0		10.1		14.0		20.0		5.8		14.3	
Ranunculus auricomus (coll.)		.		2.8		9.7		10.4		.		19.3		4.0		16.7	
Quercus robur		.		7.2		13.0		4.3		7.5		18.5		1.8		6.7	
Poa nemoralis		.		0.2		9.8		2.4		7.5		11.8		1.5		3.3	
Anemone nemorosa		.		17.7		35.8		100.0		18.3		53.3		100.0		100.0	
Fraxinus excelsior		.		7.2		2.9		43.6		1.8		4.0		62.5		24.7	
Viola hirta		.		4.0		2.9		17.5		3.3		2.5		24.0		11.0	
Fragaria vesca		.		3.3		2.0		8.1		1.5		2.5		12.8		3.3	
Rubus saxatilis		.		6.0		.		9.4		.		.		11.0		7.7	
Ribes alpinum		.		0.5		2.4		3.9		0.8		4.0		6.8		1.0	
Corylus avellana		.		.		1.4		3.0		0.8		2.0		6.0		.	
Lonicera xylosteum		.		2.3		0.3		2.0		.		1.5		4.0		.	
Hepatica nobilis		.		.		39.8		82.9		6.0		73.5		65.8		100.0	
Dentaria bulbifera		.		.		1.7		46.6		.		3.3		0.8		92.3	
Convallaria majalis		.		1.7		36.7		72.1		40.8		32.5		71.8		72.3	
Mercurialis perennis		.		.		13.0		31.1		.		26.0		0.8		61.3	
Viola riviniana		.		15.7		21.6		44.8		6.3		36.8		33.3		56.3	
Melica uniflora		.		.		1.3		25.5		.		2.5		.		51.0	
Oxalis acetosella		.		.		1.7		45.5		.		3.3		43.3		47.7	
Maianthemum bifolium		.		.		0.4		36.1		.		0.8		24.8		47.3	
Melampyrum sylvaticum		.		.		0.3		12.2		4.3		14.3		.		24.3	
Hypericum maculatum		.		2.1		2.5		10.8		2.5		2.5		2.5		19.3	
Pulmonaria officinalis		.		.		5.8		3.3		1.5		10.0		10.8		16.7	
Primula veris		.		5.5		3.3		4.3		.		6.5		0.8		7.7	
bottom layer (mean presence):																	
Dicranum scoparium		100.0		34.0		12.5		.		25.0		.		.		.	
Pleurozium schreberi		.		68.0		25.0		12.5		25.0		25.0		25.0		.	
Mnium affine		100.0		17.0		100.0		29.0		100.0		100.0		25.0		33.0	
Rhodobryum roseum		.		17.0		50.0		.		50.0		50.0		.		.	
Brachythecium rutabulum		.		17.0		25.0		12.5		.		50.0		25.0		.	

Table 9c. Environmental data and mean occurrence values in the Recent ridge vegetation groups (subgroups) (cf. Table 9a).

VEGETATIONAL GROUP – SUBGROUP		G		H		G_1		G_2		G_3	
moisture index		1-3		3-4		1-2		1		1-3	
mean relative light	(%)	97.1		59.9		92.8		100.0		98.4	
mean tree-shrub cover sum	(%)	0.1		26.1		.		.		0.3	
mean litter cover sum	(%)	5.0		24.4		15.0		.		.	
Soil depth (cm)		14.1		12.8		8.5		26.0		7.8	
horizon		H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1	H_0	H_1
soil water	H.M. (%)	2.3	0.74	1.9	0.74	2.7	1.25	1.1	0.30	3.1	0.66
	W.H.C. (%)	68.7	33.0	69.8	34.6	83.7	38.0	43.7	27.7	78.7	32.7
chemical properties	O.M. (%)	16.3	5.0	16.9	5.4	21.7	8.2	6.5	2.2	20.3	4.5
	N tot (%)	0.56	0.16	0.49	0.16	0.71	0.26	0.24	0.07	0.72	0.15
	pH (%)	5.0	-	4.7	-	4.7	-	5.2	-	5.2	-
	cond. (µmhos/cm)	167.7	98.9	177.2	103.1	151.3	93.5	114.9	60.9	236.8	142.1
	C.E.C.(meq./100 g)	19.0	5.2	18.0	5.3	25.0	7.0	7.0	2.0	25.0	6.7
	T.E.B.	10.4	-	5.0	-	8.0	-	5.0	-	18.3	-
	T.A.	9.0	1.6	13.3	3.3	18.0	4.0	2.0	.	7.1	0.7
	K^+	0.29	0.20	0.30	0.08	0.60	0.20	0.10	0.06	0.18	0.35
	Na^+	0.64	-	0.10	-	1.80	-	0.02	-	0.11	-
	Mg^{2+}	1.10	0.30	0.70	0.30	1.50	0.40	0.60	0.10	1.20	0.30
	Ca^{2+}	7.60	-	2.90	-	4.60	-	3.20	-	15.0	-
texture (%)	particles (>2 mm)	43.4	62.5	54.3	67.6	61.5	84.2	23.8	30.4	44.7	72.8
	sand	88.4	95.7	90.2	95.6	83.0	93.0	96.7	97.3	85.6	96.8
	coarse	26.3	-	27.0	-	33.1	-	25.1	-	20.7	-
	medium	54.9	-	52.0	-	41.1	-	65.5	-	58.1	-
	fine	13.7	7.8	17.3	11.1	19.7	13.4	7.4	4.9	14.0	5.1
	silt	11.0	3.6	8.2	3.8	14.5	5.0	6.0	2.7	12.4	3.2
	clay	1.7	0.2	1.6	0.7	2.5	0.5	0.7	.	2.0	.
tree-shrub layer (mean cover):											
Pinus sylvestris		.		14.0		.		.		.	
Juniperus communis		0.1		5.8		.		.		0.3	
Quercus robur		.		1.3		.		.		.	
Rosa spp.		.		0.5		.		.		.	
field layer (mean frequency):											
Veronica spicata		37.0		1.5		71.8		19.0		22.6	
Viscaria vulgaris		30.5		8.7		55.0		31.0		5.4	
Sedum acre		36.3		0.3		54.0		46.3		8.6	
Allium vineale		28.8		8.9		46.8		39.0		0.6	
Hieracium pilosella		40.0		29.7		45.3		31.3		43.4	
Poa angustifolia		13.3		23.7		25.8		7.6		6.6	
Hypericum perforatum		6.9		2.6		20.8		.		.	
Sedum maximum		6.9		2.2		20.3		.		.	
Potentilla argentea		5.6		0.3		9.0		2.3		5.4	
Festuca ovina		91.0		34.7		91.0		93.3		88.8	
Galium verum		85.0		40.2		87.5		91.0		76.6	
Achillea millefolium		80.0		32.7		63.3		90.0		86.8	
Carex arenaria		30.8		37.1		.		85.7		6.8	
Plantago lanceolata		61.3		14.6		50.0		73.3		60.6	
Phleum phleoides		29.7		7.3		21.8		65.3		2.0	
Stellaria graminea		34.6		15.7		5.0		62.0		36.8	
Rumex acetosella		55.7		7.4		54.3		56.7		56.0	
Potentilla tabernaemontanii		41.5		1.5		38.5		53.3		32.6	
Campanula rotundifolia		33.8		27.0		15.8		49.7		36.0	
Armeria maritima		31.5		2.4		20.0		48.0		26.6	
Thymus serpyllum		34.7		5.2		19.3		44.7		40.0	
Ranunculus bulbosus		25.4		1.5		.		43.7		32.6	
Anemone pratensis		22.4		13.4		4.0		43.3		20.0	
Trifolium campestre		24.2		1.1		4.2		41.0		27.4	
Pimpinella saxifraga		13.7		3.4		.		41.0		.	
Silene nutans		23.6		3.3		18.3		34.7		17.3	
Veronica arvensis		19.6		.		12.5		23.7		22.6	
Trifolium arvensis		11.7		0.3		5.3		20.0		9.2	
Arrhenatherum pratense		6.3		4.4		0.8		15.3		4.2	
Dianthus deltoides		8.6		1.5		4.3		13.7		7.4	
Agrostis tenuis		51.3		19.2		59.0		24.3		70.6	
Cerastium brachypetalum		25.3		0.7		5.0		19.0		51.8	
Lotus corniculatus		21.8		5.9		1.3		14.3		49.2	
Luzula campestris		25.0		36.3		6.3		22.3		46.0	
Aira praecox		30.7		7.5		20.0		.		42.0	
Trifolium pratense		17.6		16.0		.		14.3		38.6	
Festuca rubra		16.7		7.3		17.5		.		32.6	
Galium boreale		10.7		15.2		.		.		32.6	
Saxifraga granulata		11.8		0.3		2.5		9.0		24.0	
Bromus hordeaceus		10.5		.		0.3		10.0		20.6	
Carex caryophyllea		8.1		9.2		4.0		2.3		18.0	
Anthoxanthum odoratum		5.6		4.4		1.3		1.0		14.0	
Plantago maritima		4.6		4.1		1.3		.		12.0	
Deschampsia flexuosa		3.5		65.4		10.0		.		0.6	
Calluna vulgaris		4.2		44.7		.		.		12.6	
Rumex acetosa		4.7		25.7		10.8		.		3.4	
Veronica chamaedrys		0.2		16.8		.		.		0.6	
Carex hirta		4.6		13.7		.		9.0		4.8	
Arrhenatherum pubescens		1.9		3.6		5.8		.		.	
Hypochoeris radicata		0.7		7.5		0.8		.		1.4	
Quercus robur		0.3		7.0		0.3		.		.	
Veronica officinalis		0.7		7.0		.		.		2.0	
Juniperus communis		0.5		6.7		.		1.0		0.6	
bottom layer (mean presence):											
Dicranum scoparium		86.7		88.0		100.0		100.0		60.0	
Cladonia sp.		53.7		22.0		75.0		66.0		20.0	
Brachythecium albicans		67.0		22.0		75.0		66.0		60.0	
Mnium affine		31.7		44.0		75.0		.		20.0	
Rhytidiadelphus squarrosus		70.0		11.0		50.0		100.0		60.0	
Abietinella abietina		45.3		11.0		50.0		66.0		20.0	
Hylocomium splendens		22.0		33.0		.		66.0		.	
Hypnum cupressiforme		62.7		33.0		75.0		33.0		80.0	
Polytrichum juniperinum		39.3		22.0		25.0		33.0		60.0	
Pleurozium schreberi		8.3		66.0		25.0		.		.	

Table 10. Simple correlation coefficient (r) between the first two ordination axes and variations in different environmental factors, on each separate ridge and on the ridges together. Surface horizon (H_1) and horizon below (H_0). Significant correlation has been indicated by one asterisk (at a 5 % probability level), and high significance by two asterisks (at a 1 % probability level).

component		1				2			
ridge		A	L	R	ALR	A	L	R	ALR
relative light		-0.92**	-0.91**	-0.81**	-0.90**	0.18	0.06	0.20	0.11
tree-shrub cover sum		0.66**	0.92**	-0.73**	0.79**	-0.50**	0.14	-0.16	-0.39**
litter cover sum		0.80**	0.80**	-0.58**	0.85**	-0.16	0.14	-0.41	-0.14
soil depth		-	0.48*	-0.01	0.38	-	0.11	-0.25	0.22
horizon H_0:									
soil water	H.M.	0.34	0.14	0.11	-0.16	-0.31	0.35	0.38	-0.20
	W.H.C.	0.33	0.23	-0.03	-0.17	-0.13	0.46*	0.36	-0.23
	O.M.	0.53**	0.18	-0.08	-0.13	-0.30	0.41	0.40	-0.24*
chemical properties	Ntot	0.15	0.12	0.11	-0.29*	-0.25	0.49*	0.36	-0.26*
	pH	-0.44*	0.30	0.63**	-0.16	0.47**	0.21	0.34	0.11
	cond.	0.44*	0.25	-0.21	0.16	0.02	0.42	0.42	0.12
	particles (>2 mm)	-0.46*	-0.34	-0.22	-0.39**	-0.26	0.01	0.14	-0.07
	sand	-0.38*	0.19	0.09	-0.01	0.36*	-0.33	-0.07	0.12
	coarse	-0.31	-0.30	-0.14	-0.04	-0.38*	0.34	-0.44*	-0.17
texture	medium	0.22	0.38	0.35	0.05	0.33	-0.37	0.41	-0.08
	fine	0.29	-0.01	-0.33	0.07	0.23	-0.18	-0.20	0.34**
	silt	0.26	-0.33	-0.08	-0.05	-0.24	0.24	0.08	-0.07
	clay	0.35	0.13	-0.12	0.17	-0.34	0.28	-0.02	-0.19
horizon H_1:									
soil water	H.M.	0.12	0.10	-0.22	0.11	-0.31	0.40	0.21	-0.17
	W.H.C.	-0.08	0.21	-0.28	0.01	-0.12	0.29	-0.17	-0.16
	O.M.	0.10	0.12	-0.26	0.08	-0.31	0.32	-0.27	-0.21
chemical properties	Ntot	-0.03	0.15	-0.16	0.04	-0.17	0.29	-0.18	-0.16
	pH	-0.73**	-0.35	0.65**	-0.52**	0.40*	0.48*	0.45*	0.15
	cond.	0.23	0.12	-0.22	0.14	-0.26	0.25	0.21	-0.05
	particles (>2 mm)	-0.47**	-0.41	-0.08	-0.34**	-0.40*	-0.13	0.13	-0.17
	sand	-0.38*	0.03	0.25	-0.35**	0.40*	-0.36	0.37	0.14
	coarse	-0.37*	-0.23	-0.11	-0.08	-0.20	0.48*	-0.20	-0.20
texture	medium	-0.06	0.25	0.40	-0.15	0.35	-0.41	0.47*	-0.10
	fine	0.39*	0.20	-0.36	0.24*	0.08	-0.46*	-0.41	0.35**
	silt	0.26	-0.04	-0.20	0.32**	-0.34	0.34	-0.18	-0.13
	clay	0.39*	0.03	-0.52*	0.28	-0.32	0.14	-0.32	-0.04

Table 11a. Changes of vegetation in permanent sample plots on the Ancylus ridge. Cover degrees and phenological stages of the field layer species. Symbols: No symbol = seedling; o = vegetative; * = flowering; ● = fruiting; - = seeds dispersed; = = wilt and dry; x = presence (bottom layer species). Young lignoses have been placed in the herbaceous plant group.

Sample plot no.	1						2						3						4						5						6					
Year	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	76	77	75	76	77	
month (May, Autust)		M			A			M			A			M			A			M			A			M			A			M			A		
number of spp.	27	29	32	25	24	28	29	32	32	26	24	25	21	26	26	22	23	24	12	25	23	11	22	24	22	23	23	22	24	24	28	29	7	25	22	
habitat	dry open meadow						dry open meadow						very dry open meadow						fresh slightly shaded transitional						mesic low cover Pinus plantation						very dry open meadow					
Graminaceous plants:																																				
Agrostis tenuis	o1	o1	o1	=1	-1	●1	o1	o1	o1	=1	-1	-1	o1	o1	o1	=1	-1	-1	.	o1	o1	.	-1	●1	*4	*3	*3	●4	-4	●5	01	01	.	-1	●1	
Festuca ovina	*2	*1	*2	=2	-1	-2	*2	*2	*3	=2	-2	-3	*2	*2	*3	=2	-2	-2	.	.	.	.	.	.	.	.	.	.	.	.	1	*2	.	-1	-2	
Poa angustifolia	o1	*1	o1	=1	-1	-1	o1	o1	o1	=1	-1	-1	.	.	.	.	.	.	.	o1	.	.	-1		.	.	.	.	.	.	*1	o1	=1	-1	.	
Phleum phleoides	*2	*2	*2	=2	-2	-2	.	.	.	.	.	.	*3	o2	o1	=2	●2	-1	*1	o2	o2	=1	-2	-1	.	.	.	.	.	.	.	.	.	.	.	.	
Arrhenatherum pratense	*2	*1	*1	=2	-2	-1	.	.	.	.	.	.	.	.	.	.	.	.	*6	*6	*6	=5	-5	-5	.	.	.	.	.	.	.	.	.	.	.	
A. pubescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	.	-1	-1	.	.	.	=1	.	.	.	.	.	.	.	
Anthoxanthum odoratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*2	*2	*1	-2	-2	-1	*2	*2	.	-1	-2	
Dactylis glomerata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	o1	o2	.	.	.	.	.	.	.	.	.	.	.	
Poa nemoralis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	●1	●1	.	.	.	.	.	
Luzula campestris	.	.	o1	.	.	-1	.	.	o1	.	.	-1	●1	●1	-1	=1	-1	-1	.	●1	●1	.	-1	-.	.	.	.	.	*1	.	.	o1	.	.	o1	
Herbaceous plants:																																				
Anemone pratensis	●1	●1	●1	=1	-1	-1	●1	●1	●1	-1	-1	-1	●1	●1	●1	-2	-1	-1	●1	●1	-1	-1	-1	-1	.	.	.	.	.	.	●1	●1	-1	-1	-1	
Campanula rotundifolia	1	1	1	●1	*1	*1	o1	o1	o1	=1	*1	*1	o2	o2	o2	●3	●3	●3	.	.	1	.	.	●1	.	.	.	.	.	.	o1	1	●1	●1	1	
Plantago lanceolata	1	.	o1	=1	.	●1	.	.	*1	.	.	-1	o1	o1	o1	=1	-1	-1	*1	*1	*1	=1	-1	●1	.	.	.	.	.	.	*1	*1	-1	-1	●1	
Rumex acetosella	.	.	o1	.	.	●1	1	1	o1	=1	●1	●1	.	o1	o1	.	-1	●1	.	.	.	.	.	.	.	.	.	.	1	.	*2	*4	.	●2	●4	
Trifolium arvensis	.	o1	o1	.	●1	.	.	o1	.	.	●1	.	.	o1	.	.	●1	.	.	o1	.	.	●1	●1	.	.	.	.	.	.	o1	o1	.	●1	.	
Potentilla tabernaemontani	*2	*2	*2	=1	-2	-2	*1	*1	*1	=1	-1	-1	*1	*1	*1	-1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.	1	*1	.	-1	-1	
Galium verum	o1	o2	o2	-1	*2	*2	o1	o1	o1	=1	*1	*1	o1	o1	o1	-1	*1	*1	o4	o6	o6	-6	●6	*5	.	.	.	.	.	.	.	.	.	.	.	
Thymus serpyllum	o1	o1	o1	*1	*1	*1	o1	o1	o2	=1	●2	●2	.	o1	o1	.	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	●1	*1	
Achillea millefolium	.	.	o1	.	.	o1	o1	o1	o2	=1	*1	*1	.	.	.	.	.	.	o1	o1	o1	.	o1	o1	.	.	.	.	.	.	o1	.	.	o1	.	
Myosotis hispida	.	*1	*1	.	=1	.	*1	*1	*1	=1	.	.	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	.	.	.	
Vicia lathyroides	o1	o1	o1	.	.	.	.	*1	.	.	.	.	o1	*1	1	=1	.	●1	.	*1	*1	.	=1	.	.	.	.	.	.	.	.	.	.	.	.	
Sedum acre	o4	o3	o4	=4	-3	-3	o2	o1	o1	-2	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	-1	-1	
Veronica spicata	o1	o1	o1	*1	*2	*3	o1	o1	o1	=1	*2	*2	o1	o1	o1	=1	-1	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Artemisia campestris	o1	o1	o2	*3	*3	*3	o1	o2	o2	*3	*4	*2	o2	o2	o2	*4	*3	*3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Ranunculus bulbosus	*1	.	.	.	.	.	*1	*1	*1	.	.	.	.	.	.	.	.	.	.	o1	*2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Carex caryophyllea	o1	o1	o1	-1	-1	-1	.	.	o1	.	.	-1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Saxifraga granulata	.	.	.	.	.	.	*1	*2	*2	=1	.	.	*1	*1	*1	=1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	.	.	.	
Dianthus deltoides	.	.	.	.	.	.	.	1	1	.	.	.	.	o1	o1	=1	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	●1	*1	
Hypericum perforatum	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	●1	*1	*1	.	.	.	.	.	.	.	.	.	.	1	.	o1	o1	.	*1	*1	
Cerastium glomeratum	.	●1	●1	.	.	.	●1	●2	●1	=1	=1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	=1	=1	=1	
Veronica arvensis	.	●1	●1	.	.	.	●1	*1	●1	=1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	.	.	.	
Trifolium campestre	o1	o1	o1	=1	-1	*1	o1	o1	.	.	-1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	●1	.	.	.	.	.	
Viola riviniana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	o1	*1	*1	o1	-1	-1	o1	.	.	.	.	.	
Melampyrum cristatum	.	.	o1	.	.	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	●1	.	.	.	.	.	.	.	.	.	.	.	.	
Silene nutans	.	.	.	.	.	.	*1	*1	o1	-1	-1	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	o1	.	o1	o1	
Pimpinella saxifraga	.	.	.	.	.	.	o1	o1	1	*1	*1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	●1	*1	*1	
Knautia arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	*1	.	.	.	.	.	
Veronica chamaedrys	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*8	o1	o1	=1	o1	o2	o3	o1	o2	-2	o1	o1	.	.	.	.	.	
Stellaria holostea	.	.	.	.	.	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●4	*2	*1	=1	-1	-1	.	.	.	.	.	
Prunus spinosa	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	o1	o1	o1	.	.	.	.	.	.	o2	o2	o3	o2	o3	o3	.	.	.	.	.	
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	=1	o1	o1	o1	o1	o1	o1	o1	.	-1	-1	
Hieracium pilosella	o1	o1	o1	-1	-1	-1	o2	o2	o2	-2	-2	-2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Veronica officinalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	
Adoxa moschatellina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	-7	●4	●5	.	.	.	.	.	.	.	.	.	
Erophila verna	.	.	.	.	.	.	.	●1	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	-1	.	=1	.	
Taraxacum spp. (Vulg.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	.	.	.	.	.	.	.	.	.	*1	*1	.	.	.	
Potentilla argentea	o1	o1	o1	-1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Jasione montana	.	.	.	.	.	.	.	.	●1	.	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Helianthemum nummularium	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Lotus corniculatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	o1	o1	
Geranium sanguineum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	o1	o1	.	.	.	.	.	.	.	.	.	.	.	
Allium vineale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	●1	.	.	.	.	.	.	.	.	.	.	.	.	
Trifolium repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	=1	-1	.	
Quercus robur	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	
Viola canina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	o1	-1	-1	●1	.	.	.	.	.	
Fraxinus excelsior	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o2	o2	o1	o2	o3	.	.	.	.	.	
Lactuca muralis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	*1	.	.	.	.	.	.	.	
Rubus corylifolius (coll.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o2	o1	-1	●2	-2	.	.	.	.	.	
Rubus ideaus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o2	-1	-1	*2	.	.	.	.	.	

Table 11a (contin.)

sample plot no.	1						2						3						4						5						6					
year	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	76	77	75	76	77
month (May, August)		M			A			M			A			M			A			M			A			M			A			M			A	
Rubus saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o2	-1	-1	-1	.	.	.	.	.	.
Hepatica nobilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-1	-2	-1	o1	o1	o2	.	.	.	.	.	.
Anemone nemorosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	•1	.	.	.	.	.	.	.	.	.	.
Calium boreale	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala amarella	.	•1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arenaria serpyllifolia	.	.	.	.	.	.	o1	.	.	=1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza sambucina	.	.	.	.	.	.	.	•1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia hirsuta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	=3	=1	.	-1	•1	.	.	.	.	.	.	.	.	.	.	.	.
Mosses and lichens:																																				
Rhytidiadelphus squarrosus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	x	.	.	x
Cladonia sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	x	x
Campothecium lutescens	x	.	.	x	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	x	x	x	x	.	x	x
Abietinella abietina	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brachythecium albicans	x	x	x	x	x	x	.	.	.	.	.	.	.	x	x	.	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.
Climacium dendroides f. dep	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	x	x	.	.	.	.	.	.	.	.	.	.	.
Mnium affine	x	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.
Hypnum cupressiforme	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum juniperinum	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirriphyllum piliferum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.
Rhodobryum roseum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
Pleurozium schreberi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Eurhynchium zetterstedtii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Rhytidiadelphus triquetrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	x	.	.	.	.	.	.	.
Hylocomium splendens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Brachythecium rutabulum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Pohlia nutans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Lophocolea heterophylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.
Ceratodon purpureus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	x	x
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Others:																																				
Agaricus 1	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 11b. Changes of vegetation in permanent sample plots on the Litorina ridge.

sample plot no.	1			2			3			4			5		
year	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77
month (May, August)	M			A			M			A			M		A
number of spp.	21	22	22	18	20	19	13	15	15	12	15	16	29	30	31
habitat type	dry mesic deciduous			low cover forest			dry shaded glade						dry open meadow		

Graminaceous plants:																												
Anthoxanthum odoratum	*1	*1	*1	=1	-1	-1	*1	*1	*1	=1	-1	-1	.	.	.	.	.	.	*1	.	o1	=1	.	-1	*2	*2	*2	=2	-1	-2
Agrostis tenuis	*6	o5	o5	-6	•6	•6	.	*1	*1	.	-1	•1	o1	o1	o1	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Festuca ovina	.	.	.	.	.	.	*3	*2	*2	=3	-3	-3	*3	*2	*2	=4	-2	-2	.	.	.	.	.	.	*1	*1	*1	=1	-1	-1
Melica nutans	*1	*1	*1	-1	-2	-2	.	.	.	.	.	.	.	.	.	.	.	.	*4	*4	o2	-2	•4	•2	.	.	.	.	.	.
Poa angustifolia	.	.	.	.	.	.	1	*1	*1	=1	-1	-1	.	o1	o1	.	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Dactylis glomerata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	o1	o1	.	.	o1	.	.	o1	.	.	.	.	.	.
Festuca rubra	.	.	.	.	.	.	.	.	.	.	.	.	*2	*1	*1	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Arrhenatherum pratense	.	.	.	.	.	.	.	.	.	.	.	.	*2	*2	*2	=2	-2	-2	.	.	.	.	.	.	.	.	.	.	.	.
Phleum phleoides	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	=1	-1	•1	.	.	.	.	.	.	.	.	.	.	.	.
Arrhenatherum elatius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	o1	o1	-1	-1	-1	.	.	.	.	.	.
Deschampsia flexuosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	o1	o1	-2	•1	•1
Luzula campestris	*1	*1	*2	=1	-1	-1	.	.	.	.	.	.	*2	•1	*2	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Herbaceous plants:																												
Melampyrum pratense	o4	o1	o1	=1	*2	*2	o1	.	.	.	.	.	.	.	.	.	.	.	o6	o2	o1	=1	•1	•1	o1	o1	o1	-1	•1	-1
Achillea millefolium	o1	o1	o1	o1	o1	o1	1	o1	o1	o1	o1	o1	o1	o1	o1	=1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.
Campanula rotundifolia	.	1	1	.	o1	.	1	o1	o1	•1	*1	*1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Convallaria majalis	*5	*5	*6	-5	-5	-6	o1	o1	o1	=1	-1	-1	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.
Veronica spicata	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.
Silene nutans	.	.	.	.	.	.	o1	*1	o1	-1	-1	*1	*1	o1	o1	=1	o1	*1	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium	.	.	.	.	.	.	.	.	.	.	.	.	o4	o3	o4	=3	•2	*4	.	.	.	.	.	.	o1	o1	o1	-1	*1	*1
Knautia arvensis	.	.	o1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	*1	.	.	.	.	.	.	.
Veronica chamaedrys	o1	o1	o1	=1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	-1	o1	o1	.	.	.	.	.	.
Allium vineale	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	-1	.	.	o1	o1	.	.	.	.	.	.	.	.	.
Quercus robur	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1
Stellaria holostea	*2	*2	*2	-1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.	*4	*2	*2	-2	-1	-1	.	.	.	.	.	.
Hepatica nobilis	-1	-1	-1	o1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	-1	-2	-2	o2	o2	o2	.	.	.	.	.	.
Anemone nemorosa	-2	-2	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-1	.	.	.	.	.	.	.	.	.
Lathyrus montanus	*1	*1	*1	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.
Calluna vulgaris	o3	o2	o3	*3	*2	*3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	o1	.	.
Trifolium montanum	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	o1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla tabernaemontani	.	.	.	.	.	.	.	.	.	.	.	.	•1	*1	*1	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Galium verum	.	.	.	.	.	.	.	.	.	.	.	.	o3	o1	o2	*2	*2	*2	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus bulbosus	.	.	.	.	.	.	.	.	.	.	.	.	*1	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thymus serpyllum	.	.	.	.	.	.	o1	o1	o2	-1	•1	•2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex caryophyllea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.
Plantago lanceolata	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	*1	=1	-1	-1	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga granulata	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	*1	=1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum	.	o1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sanguineum	.	.	.	.	.	.	.	.	.	.	.	.	o8	o8	o7	-8	•8	•8	.	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	-1	o1	o1	.	.	.	.	.	.
Rubus saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	o1	o1	.	.	.	.	.	.
Viola riviniana	.	.	1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica officinalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	-1	o1	o1	.	.	.	.	.	.
Trifolium medium	o3	o3	o2	-3	-5	•6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fragaria vesca	1	o1	.	=1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Filipendula vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	=1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.
Armeria maritima	.	.	.	.	.	.	.	.	.	.	.	.	1	.	o1	-1	.	o1	.	.	.	.	.	.	.	.	.	.	.	.
Antennaria dioica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.
Corylus avellana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Primula veris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*2	*3	*3	-2	-3	-3	.	.	.	.	.	.
Ranunculus auricomus coll.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	o1	.	.	o1	.	.	.	.	.	.	.
Anthriscus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*2	o6	o8	-1	-5	-3	.	.	.	.	.	.
Campanula persicifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	•1	•1	•1	.	.	.	.	.	.
Vicia cracca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	o1	o1	-2	-2	-2	.	.	.	.	.	.
Geum urbanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	-1	•1	•1	.	.	.	.	.	.
Valeriana officinalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	o1	o1	.	.	.	.	.	.
Chamaenerion angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	o1	.	.	.	.	.	.	.
Galium aparine	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	.	.	.	.	.	.	.	.

Table 11b (contin.)

sample no.	1						2						3						4						5					
year	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77
month (May, August)		M			A			M			A			M			A			M			A			M			A	
Melampyrum sylvaticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	●1	●1	.	.	.	.	.	.
Solidago virgaurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	*1	.	.	.	.	.	.
Ranunculus ficaria	-2	-4	●4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adoxa moschatellina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-1	-1	.	.	.	.	.	.	.	.	.
Myosotis hispida	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium glomeratum	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium campestre	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia lathyroides	.	.	.	.	.	.	.	.	.	.	.	.	.	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza sambucina	.	.	.	.	.	.	.	.	.	.	.	.	●1	*1	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia hirsuta	.	.	.	.	.	.	.	.	.	.	.	.	*1	*1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum spp. (Vulg.)	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mosses and lichens:																														
Mnium affine	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.
Pleurozium schreberi	.	.	.	.	.	.	x	x	x	x	x	x	x	.	.	x	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Dicranum polysetum	.	.	.	.	.	.	.	x	x	.	x	x	x	.	.	x	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Brachythecium albicans	.	.	.	.	.	.	.	x	x	.	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Rhytidiadelphus squarrosus	x	x	x	x	x	x	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum juniperinum	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Rhodobryum roseum	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.
Brachythecium rutabulum	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.
Dicranum scoparium	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Climacium dendroides f. dep.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Hylocomium splendens	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia spp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
C. sylvatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Cetraria islandica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
others:																														
Agaricus 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.

Table IIc. Changes of vegetation in permanent sample plots on the Recent ridge.

sample plot no.	1						2						3						4						5					
year	75	76	77	75	76	77	75	76	77	75	76	77	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77
month (May, August)		M			A			M			A			M			A			M			A			M			A		
number of spp.	18	24	23	17	20	22	23	23	22	20	23	22	13	15	12	15	15	19	17	17	17	17	17	21	22	25	20	21	21			
habitat type	dry open meadow						dry slightly shaded meadow						dry mesic shaded glade						dry open meadow						very dry open meadow					
Graminaceous plants:																																
Festuca ovina	+5	+5	+5	=5	−5	−5	+5	+5	+4	5	−5	−5	+1	+1	=1	−1	−.	+6	+5	+5	6	+6	+6	+6	+6	+7	=6	+6	+6			
Deschampsia flexuosa	.	.	.	.	.	.	o2	o2	o2	2	−1	●1	o1	+3	3	−2	●2	.	.	.	.	.	.	.	.	.	.	.	.			
Festuca rubra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+1	.	.	−1	.	+1	+1	.	−1	−1			
Agrostis tenuis	o1	o1	o1	=1	1	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Arrhenatherum pratense	.	o1	.	.	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Phleum phleoides	+1	−1	+1	1	−1	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Anthoxanthum odoratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+1	+1	+1	=1	−1	−1	.	.	.	.	.	.			
Poa angustifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	−1	−1	−1			
Luzula campestris	.	.	.	.	.	.	−1	−1	−1	.	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	.	o1			
Herbaceous plants:																																
Hieracium pilosella	o1	o1	o1	1	1	−1	o1	o1	o1	+1	−1	−.	.	o1	.	o1	.	o2	o1	o1	=2	1	−1	o1	.	o1	.	.	.			
Galium verum	o1	o1	o1	●1	+1	+1	o1	o1	o1	●1	+1	+1	.	.	.	.	.	o1	o1	o1	●1	+1	+1	o2	o2	o1	−1	+2	+1			
Rumex acetosella	+1	−1	+1	+1	1	−1	+1	−1	−2	.	−1	●2	.	.	.	.	.	o1	o1	+1	−1	−1	●1	+2	+2	+2	−1	−1	−1			
Campanula rotundifolia	o1	o1	o1	=1	+1	−1	o1	o1	o1	+1	+1	+1	.	.	.	.	.	.	.	.	.	.	.	o2	o1	o1	=1	+1	+1			
Anemone pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	●1	●1	o1	o1	o1	●2	+2	●1	=2	o2	o2			
Veronica spicata	.	.	.	.	.	.	.	.	.	−1	.	.	.	.	.	.	.	o1	.	.	−1	.	.	.	.	.	.	.	.	.			
Achillea millefolium	o1	o1	o1	1	o1	o1	o1	o1	o1	=1	+1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Hypericum perforatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o2	o1	o1	=2	●1	+1	o1	o1	o1	=1	●1	o1			
Allium vineale	o1	o1	o1	.	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	−1	.			
Carex hirta	.	.	o1	.	.	o1	o1	o1	o1	o1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Plantago maritima	o1	o1	o1	●1	●1	+1	o1	o1	o1	●1	+1	●1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Calluna vulgaris	.	.	.	.	.	.	o3	o2	o3	+3	+2	+3	o1	o1	+2	+1	+1	.	.	.	.	.	.	.	.	.	.	.	.			
Viscaria vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+3	+3	+3	3	−3	−3	+1	o1	+1	1	−1	−1			
Sedum maximum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	−1	o1	.	.	1	1	1	o1	+1			
Armeria maritima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	.	−1	+1	o1	+1	o1	−1	●1	+1			
Lotus corniculatus	.	.	.	.	.	1	+1	o1	o1	●1	+1	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Potentilla tabernae montani.	.	.	.	.	.	.	−1	1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Artemisia campestris	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Thymus serpyllum	.	o1	o1	.	o1	+2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Plantago lanceolata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	.	.	.	.			
Saxifraga granulata	.	+1	+1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Pimpinella saxifraga	o1	o1	o1	−1	+1	+1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Helianthemum nummularium	+5	+5	o5	4	●3	+5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Sedum acre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	1	−1	−1			
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	o1	=1	o1	o1	.	.	.	.	.	.			
Veronica officinalis	.	.	.	.	.	.	.	.	o1	.	.	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Galium boreale	.	.	.	.	.	.	o1	o1	o1	−1	●1	+1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Carex arenaria	o1	o1	o1	1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Vicia cracca	.	.	.	.	.	.	o1	o1	o1	=1	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Hypochoeris radicata	.	.	.	.	.	.	o1	o1	o1	1	1	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Trifolium pratense	.	.	.	.	.	.	o1	o1	1	−1	−1	o1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Filipendula vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	.	.	.	.	.	.	.	.	.	.			
Turrtis glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	.	+1	1	.	−1			
Euphrasia spp.	.	.	1	.	.	+1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Melampyrum pratense	.	.	.	.	.	.	.	.	.	.	.	.	o1	o1	.	●1	o1	.	.	.	.	.	.	.	.	.	.	.	.			
Convallaria majalis	.	.	.	.	.	.	.	.	.	.	.	.	.	o1	.	o1	o1	.	.	.	.	.	.	.	.	.	.	.	.			
Veronica arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	−1	●1	+1	=1	●1	.			
Erophila verna	.	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Dactylorhiza sambucina	.	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Taraxacum spp. (Vulg.)	.	−1	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Stellaria graminea	.	.	.	.	.	.	.	o1	.	.	−1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
Arabidopsis thaliana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	●1	●1	.	.	.			

Table 11c (contin.)

sample plot no.	1						2						3					4						5				
year	75	76	77	75	76	77	75	76	77	75	76	77	76	77	75	76	77	75	76	77	75	76	77	75	76	77	75	76	77
month (May, August)		M			A			M			A			M		A			M			A			M			A	
Mosses and lichens:																													
Dicranum scoparium	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladonia spp.	x	x	x	x	x	x	.	.	.	.	.	.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
C. sylvatica	.	.	.	.	.	.	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	x	x	x	x	x	x
Ceratodon purpureus	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Brachythecium albicans	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.
Rhytidiadelphus squarrosus	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.
Hypnum cupressiforme	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	.	.	.	.	.	.	x	x	x	x	x	x
Polytrichum juniperinum	.	.	.	.	.	.	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Pleurozium schreberi	.	.	.	.	.	.	x	x	x	x	x	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Abietinella abietina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Mnium affine	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.
Rhodobryum roseum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	x
Hylocomium splendens	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum polysetum	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
Cornicularia aculeata	.	.	.	.	.	.	x	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cetraria islandica	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.	.
others:																													
Agaricus 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.

Table 12. Standing crop of living graminaceous and herbaceous plants, total living material, and dead material; in four harvest plots (no previous harvests). Values in g per 1/16 m^2 (oven dry weight). Summer total (May-August) and autumn total (September and October) values of standing crop are given for each category.

harvest year (no earlier harvest)		1975				1976				1977			
		gram.	herb.	liv.	dead	gram.	herb.	liv.	dead	gram.	herb.	liv.	dead
Ancylus open meadow	May	5.1	10.2	15.3	6.0	2.4	5.9	8.3	5.5	3.4	9.9	13.3	3.8
	June	2.6	4.4	7.0	7.8	3.9	9.9	13.8	5.1	4.2	8.7	12.9	4.5
	July	2.4	3.2	5.6	7.4	5.9	10.5	16.4	6.2	4.7	7.9	12.6	7.1
	Aug	0.2	1.4	1.6	9.8	4.2	12.1	16.3	8.0	3.3	10.0	13.3	6.0
summer T		10.3	19.2	29.5	31.0	16.4	38.4	54.8	24.8	15.6	36.5	52.1	21.4
	Sept	2.0	3.6	5.6	13.8	3.0	3.1	6.1	7.9	1.2	4.7	5.9	10.6
	Oct	1.1	5.3	6.4	9.5	1.9	7.6	9.5	14.8	1.4	7.4	8.8	11.1
autumn T		3.1	8.9	12.0	23.3	4.9	10.7	15.6	22.7	2.6	12.1	14.7	21.7
Recent open meadow	May	10.2	3.6	13.8	6.3	4.3	3.6	7.9	8.9	8.6	4.5	13.1	9.0
	June	3.7	4.7	8.4	9.3	11.9	2.6	14.5	8.7	11.3	4.6	15.9	11.4
	July	1.2	2.3	3.5	8.2	10.1	9.0	19.1	19.5	8.9	3.5	12.4	5.8
	Aug	1.1	1.3	2.4	11.1	7.8	8.2	16.0	8.4	9.6	4.3	13.9	12.4
summer T		16.2	11.9	28.1	34.9	34.1	23.4	57.5	45.5	38.4	16.9	55.3	38.6
	Sept	2.1	3.2	5.3	10.5	6.4	1.6	8.0	13.2	7.6	7.5	15.1	9.5
	Oct	4.1	2.0	6.1	18.1	4.2	2.9	7.1	20.6	2.4	0.8	3.2	12.7
autumn T		6.2	5.2	11.4	28.6	10.6	4.5	15.1	33.8	10.0	8.3	18.3	22.2
Litorina open meadow	May	1.3	9.8	11.1	0.5	1.6	7.8	9.4	7.1	2.2	7.2	9.4	3.6
	June	0.6	16.4	17.0	2.0	2.4	13.0	15.4	4.3	10.9	8.5	19.4	9.8
	July	0.5	8.9	9.4	4.5	3.8	27.7	31.5	7.9	4.0	18.2	22.2	3.5
	Aug	0.4	2.6	3.0	8.6	4.2	16.9	21.1	8.9	2.6	15.2	17.8	3.2
summer T		2.8	37.7	40.5	15.6	12.0	65.4	77.4	28.2	19.7	49.1	68.8	20.1
	Sept	1.4	3.9	5.3	11.8	1.4	3.7	5.1	8.5	4.3	13.3	17.6	12.7
	Oct	1.3	4.8	6.1	10.5	1.3	3.7	5.0	12.6	1.3	7.8	9.1	13.3
autumn T		2.7	8.7	11.4	22.3	2.7	7.4	10.1	21.1	5.6	21.1	26.7	26.0
Litorina low-cover forest	May	3.7	2.8	6.5	3.1	2.0	2.3	4.3	10.1	5.5	3.1	8.6	4.0
	June	5.9	4.1	10.0	5.0	3.0	3.3	6.3	3.3	4.9	4.3	9.2	7.0
	July	5.3	4.2	9.5	5.0	6.8	3.8	10.6	7.5	5.4	3.9	9.3	2.8
	Aug	3.7	0.8	4.5	7.1	5.7	3.4	9.1	5.1	8.1	5.6	13.7	5.6
summer T		18.6	11.9	30.5	20.2	17.5	12.8	30.3	26.0	23.9	16.9	40.8	19.4
	Sept	3.0	1.1	4.1	8.4	4.5	2.3	6.8	5.5	6.2	2.3	8.5	6.0
	Oct	1.6	0.9	2.5	7.8	2.8	0.8	3.6	11.2	4.0	2.0	6.0	9.2
autumn T		4.6	2.0	6.6	16.2	7.3	3.1	10.4	16.7	10.2	4.3	14.5	15.2

Table 13. Repeated harvests in four sample plots (for other information see Table 12).

harvest year (earlier harvest)		1977 (1975)				1976 (1975)				1977 (1976)				1977 (1975,1976)			
		gram.	herb.	liv.	dead	gram.	herb.	liv.	dead	gram.	herb.	liv.	dead	gram.	herb.	liv.	dead
Ancylus	May	4.1	6.0	10.1	4.9	1.4	4.8	6.2	1.9	2.0	4.6	6.6	1.3	2.5	3.5	6.0	2.1
open	June	1.7	7.2	8.9	2.0	1.6	6.4	8.0	2.7	1.5	3.8	5.3	2.1	1.7	7.5	9.2	3.2
meadow	July	2.6	9.3	11.9	2.7	1.6	9.5	11.1	2.6	1.8	7.0	8.8	3.8	1.5	6.3	7.8	2.6
	Aug	2.3	7.1	9.4	6.3	1.8	7.4	9.2	3.5	3.7	6.1	9.8	8.0	1.2	6.6	7.8	2.1
	summer T	10.7	29.6	40.3	15.9	6.4	28.1	34.5	10.7	9.0	21.5	30.5	15.2	6.9	23.9	30.8	10.1
	Sept	5.1	3.9	9.0	12.4	1.6	4.8	6.4	2.6	0.7	5.0	5.7	9.9	0.5	2.2	2.7	7.8
	Oct	0.6	1.1	1.7	9.2	1.0	3.2	4.2	6.6	0.8	0.1	0.9	3.8	0.5	3.2	3.7	6.4
	autumn T	5.7	5.0	10.7	21.6	2.6	9.0	10.6	9.2	1.5	5.1	6.6	13.7	1.0	5.4	6.4	14.2
Recent	May	3.6	3.4	7.0	1.6	1.3	2.0	3.3	1.4	2.0	3.6	5.6	1.8	4.4	3.7	8.1	1.2
open	June	4.9	4.2	9.1	4.8	3.7	2.0	5.7	2.1	4.2	1.6	5.8	2.6	3.2	1.8	5.0	2.2
meadow	July	4.5	6.2	10.7	3.6	3.4	4.9	8.3	2.6	3.4	2.8	6.2	1.4	1.4	1.4	2.8	2.9
	Aug	11.0	3.4	14.4	11.8	3.6	5.8	9.4	4.7	7.8	2.2	10.0	4.2	5.6	2.6	8.2	1.2
	summer T	24.0	17.2	41.2	21.8	12.0	14.7	26.7	10.8	17.4	10.2	27.6	10.0	14.6	9.5	24.1	7.5
	Sept	1.7	2.6	4.3	7.7	0.9	1.2	2.1	7.9	7.6	1.4	9.0	3.8	1.5	3.1	4.6	3.7
	Oct	0.9	0.8	1.7	8.4	2.6	1.3	3.9	7.9	3.0	0.7	3.7	5.5	1.3	1.6	2.9	3.4
	autumn T	2.6	3.4	6.0	16.1	3.5	2.5	6.0	15.8	10.6	2.1	12.7	9.3	2.8	4.7	7.5	7.1
Litorina	May	3.7	4.6	8.3	3.2	0.6	4.7	5.3	2.2	1.1	5.8	6.9	1.2	1.3	6.7	8.0	1.2
open	June	0.9	10.0	10.9	2.1	1.0	7.5	8.5	1.3	1.8	6.0	7.8	1.1	0.4	6.0	6.4	0.8
meadow	July	1.8	11.0	12.8	2.2	1.7	12.1	13.8	1.4	1.0	8.7	9.7	1.2	1.2	7.2	8.4	1.7
	Aug	2.5	14.6	17.1	2.9	2.2	10.7	12.9	3.7	2.0	9.4	11.4	1.9	2.4	9.8	12.2	2.2
	summer T	8.9	40.2	49.1	10.4	5.5	35.0	40.5	8.6	5.9	29.9	35.8	5.4	5.3	29.7	35.0	5.9
	Sept	0.3	5.3	5.6	6.3	0.7	2.0	2.7	4.7	0.9	3.2	4.1	5.8	0.8	4.4	5.2	3.3
	Oct	0.5	3.6	4.1	8.5	0.8	3.7	4.5	11.5	0.8	4.8	5.6	4.2	0.8	3.0	3.8	10.0
	autumn T	0.8	8.9	9.7	14.8	1.5	5.7	7.2	16.2	1.7	8.0	9.7	10.0	1.6	7.4	9.0	13.3
Litorina	May	1.3	2.1	3.4	2.3	1.8	1.0	2.8	6.9	1.7	1.8	3.5	2.1	0.8	1.0	1.8	0.7
low-cover	June	5.4	2.6	8.0	2.5	2.0	1.5	3.5	2.5	3.9	2.1	6.0	1.3	2.4	1.4	3.8	0.8
forest	July	4.3	3.1	7.4	3.9	2.6	1.5	4.1	1.4	2.9	1.5	4.4	0.5	3.8	1.3	5.1	1.2
	Aug	6.9	1.4	8.3	4.9	3.0	1.6	4.6	1.3	6.3	3.0	9.3	1.2	5.5	2.9	8.4	2.5
	summer T	17.9	9.2	27.1	13.6	9.4	5.6	15.0	12.1	14.8	8.4	23.2	5.1	12.5	6.6	19.1	5.2
	Sept	3.8	0.9	4.7	4.5	1.5	0.4	1.9	1.1	1.8	2.0	3.8	2.4	0.6	1.4	2.0	1.8
	Oct	1.6	0.6	2.2	3.2	1.8	0.5	2.3	4.4	1.1	0.8	1.9	4.6	1.0	0.1	1.1	4.6
	autumn T	5.4	1.5	6.9	7.7	3.3	0.9	4.2	5.5	2.9	2.8	5.7	8.0	1.6	1.5	3.1	6.4

Table 14. Some characteristics of four harvests plots (10 x 10 m) on the Ancylus, Litorina, and Recent ridge; with information on sampling and environmental conditions. The material obtained by repeated harvests and the seasonal aspects are expressed as percentage of the total standing crop (in summer 1977) including living graminaceous and herbaceous plants and dead material. The summer 1977 total of standing crop was taken to be 100 %.

ridge	A open meadow	R open meadow	L open meadow	L low cover forest
rel. light %	94	93	100	44
soil depth (cm)	50	7	21	31
soil water:				
W.H.C. (%)	46.5	84.9	54.1	50.5
chemical properties:				
O.M. (%)	6.4	23.0	9.6	6.5
Ntot (%)	0.26	0.86	0.41	0.19
pH	5.4	4.4	4.9	4.9
cond. (µ mhos/cm)	131.0	201.3	169.4	126.3
K^+ (meq./100 g)	0.2	0.6	0.1	0.02
Na^+ -"-	0.05	1.8	0.04	0.04
Mg^{2+} -"-	0.6	1.5	1.3	0.4
Ca^{2+} -"-	3.6	4.6	8.8	2.8
texture (%):				
particles (>2 mm)	3.3	87.8	24.4	0.7
sand	94	84	84	92
silt	4	14	14	6
clay	2	2	2	2
total plant cover (%)*:				
graminaceous plants	61.7 (1975)	72.6 (1975)	38.3 (1976)	71.0 (1976)
herbaceous plants	83.4	61.0	180.4	57.5

season (summer, autumn)	summ.	aut.	summ.	aut.	summ.	aut.	summ.	aut.
harvest of 1977 (no earlier harvest)								
stand. crop	100	50	100	43	100	59	100	49
gram. plants	21	4	41	11	22	6	40	17
herb. plants	50	16	18	9	55	24	28	7
living mat.	71	20	59	20	77	30	68	24
dead mat.	29	30	41	23	23	29	22	25
harvest of 1977 (earlier harvest 1975)								
stand. crop	77	44	67	24	67	28	68	24
gram. plants	15	8	26	3	10	1	30	9
herb. plants	40	7	18	4	45	10	15	2
living mat.	55	15	44	7	55	11	45	11
dead mat.	22	29	23	17	12	17	23	13
harvest of 1977 (earlier harvest 1976)								
stand. crop	62	28	40	23	46	22	47	23
gram. plants	12	2	19	11	7	2	25	5
herb. plants	29	7	11	2	33	9	14	5
living mat.	41	9	30	13	40	11	39	10
dead mat.	21	19	10	10	6	11	8	13
harvest of 1977 (earlier harv. 1975, 1976)								
stand. crop	56	28	34	16	46	25	40	16
gram. plants	9	2	16	3	6	2	21	3
herb. plants	33	7	10	5	33	8	11	2
living mat.	42	9	26	8	39	10	32	5
dead mat.	14	19	8	8	7	15	8	11

*Species which attain >5 % as cover value (A in 1975; others in 1976):

A (open meadow): Festuca ovina (24.2), Agrostis tenuis (19.5), Thymus serpyllum (14.9), Veronica spicata (12.9), Galium verum (12.7), Arrhenatherum pratense (10.7), Potentilla tabernae (10.2), Poa angustifolia (8.0), Campanula rotundifolia (5.8).

R (open meadow): Festuca ovina (29.3), Hypericum perforatum (10.8), Agrostis tenuis (10.8), Galium verum (8.5), Poa angustifolia (8.5), Hieracium pilosella (8.2), Viscaria vulgaris (6.5), Achillea millefolium (6.0), Deschampsia flexuosa (5.0).

L (open meadow): Geranium sanguineum (43.3), Helianthemum nummularium (37.7), Veronica spicata (11.0), Filipendula vulgaris (9.8), Luzula campestris (8.8), Allium vineale (8.0), Plantago lanceolata (7.5), Festuca rubra (7.2), Festuca ovina (6.5), Galium verum (6.0).

L (low cover forest): Deschampsia flexuosa (33.2), Melica nutans (24.2), Stellaria holostea (18.7), Veronica chamaedrys (8.7), Agrostis tenuis (7.2), Convallaria majalis (6.2), Galium verum (5.0),+ tree-shrub species: Quercus robur (50.7).

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